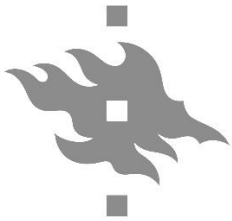


Master's thesis

Palaeobiology and Palaeoclimatology

Changes in peatland vegetation dynamics and their link to climate in a southern boreal bog during the last centuries

Miika Huilla

2020

Supervisors:
Minna Väliranta
Eeva-Stiina Tuittila

Master's Programme in Geology and Geophysics

Faculty of Science

Tiedekunta – Fakultet – Faculty
Matemaattis-Luonnontieteellinen tiedekunta

Koulutusohjelma – Utbildingsprogram – Degree Programme
Geotieteiden ja maantieteen osasto

Tekijä – Författare – Author
Miika Huilla

Työn nimi – Arbetets titel – Title
Changes in peatland vegetation dynamics and their link to climate in a southern boreal bog during the last centuries

Oppiaine/Opintosuunta – Läroämne/Studieinriktning – Subject/Study track
Geologia

Työn laji – Arbetets art – Level	Aika – Datum – Year	Sivumäärä – Sidoantal – Pages
Pro Gradu	2020	54

Tiivistelmä – Referat – Abstract

Pohjoiset suot muodostavat globaalisti merkittävän hiilinielun varastoiden lähes kolmanneksen maapallon maaperään sitoutuneesta hiilestä. Suot ovat jatkuvassa yhteydessä ilmakehään ja jos ilmastossa tai ympäristössä tapahtuu muutoksia voivat suot jopa muuttua hiilinieluista hiilen lähteiksi. Ilmasto on tärkein soiden ja niiden hiilidynamiikan kontrolloija. Lämpenevän ilmaston on ennustettu aiheuttavan jatkuvasti voimakkaampia muutoksia, ja nämä koskevat myös soita. Suot ovat ympäristönä määritelty niille ominaisen kasvillisuuden perusteella. Suokasvillisuus ei ole staattinen, vaan sen sijaan jatkuvassa muutoksessa reagoidessaan ilmastoon. Muutokset suokasvillisuudessa ilmenevät suon kasvillisuusyhteisöjen muutoksina.

Tutkin tässä työssä suokasvillisuuden ilmastovastetta Lakkasuo nimisellä rahkasuolla eteläisessä Suomessa. Korkea resoluutioisen makrofossiillianalyysin avulla kasvillisuuden muutoksia tutkittiin aikasidonnaisesti. Tarkat ajoitukset tehtiin ^{210}Pb ja ^{14}C menetelmillä. Turpeen tiheys sekä hiili-typpisuhde analysoitiin, hiilen kertymä laskettiin ja nykyinen kasvillisuus ja vedenpinnantaso kirjattiin maastotöiden yhteydessä. Kolme 50-60cm pitkää turvenäytettä analysoitiin. Ajoituksen perusteella vanhimmat näytteet olivat n. 300 vuoden ikäisiä. Eri turvesarjojen ajassa tapahtuvia kasvilajiston muutoksia tulkittiin tilastollisen Changepoint-menetelmän avulla.

Koska vedenpinnantaso määrittää rahkasoiden kasvillisuusyhteisöjä, kiinnittyi huomio tutkimuksessa Lakkasuon aiempiin kosteusolosuhteisiin. Kolme suon mikrohabitaattia, jotka tällä hetkellä edustavat eri vedenpinnantasoja, valittiin tutkimuksen kohteeksi. Kasvillisuuden muutoksia tarkasteltiin yksittäisten lajien ohella suurempina ryhminä. Ryhmiin kasvilajit jaettiin niiden suosiman kosteusympäristön mukaan: ”kuiva”, ”välipinta” tai ”märkä”.

Muutokset kosteusolosuhteissa näkyivät selvinä muutoksina Lakkasuon kasviyhteisössä. Muutokset pystyttiin yhdistämään suuriin ilmastovaiheisiin pieneen jääkauteen ja nykyiseen lämpenemiseen. Pienen jääkauden aikana suolla vallitsivat märemmät olosuhteet, ja näytteissä esiintyi jäänteitä niihin sopeutuneista kasveista, kun taas nykyinen lämpeneminen on suosinut kuivempien olosuhteiden lajistoa. Tästä voidaan päätellä, että viimeisen n. 300 vuoden aikana ilmasto on baikuttanut Lakkasuon kasviyhteisöihin kosteusolosuhteiden muutoksien kautta. Nykyinen kehitys kohti kuivempaa suota tulee vaikuttamaan Lakkasuon hiilidynamiikkaan. Suon hiilensitomiskyvyn ennustetaan laskevan efektiivisen kosteuden laskiessa tulevaisuuden lämpenevässä ilmastossa.

Avainsanat – Nyckelord – Keywords
boreaaliset suot, ilmastonmuutos, ympäristön muutos, suokasvillisuus, kasvimakrofossiilit

Ohjaaja tai ohjaajat – Handledare – Supervisor or supervisors
Minna Väliranta
Eeva-Stiina Tuittila

Säilytyspaikka – Förvaringställe – Where deposited

Muita tietoja – Övriga uppgifter – Additional information

Tiedekunta – Fakultet – Faculty
Faculty of Science

Koulutusohjelma – Utbildingsprogram – Degree Programme
Department of Geosciences and Geography

Tekijä – Författare – Author
Miika Huilla

Työn nimi – Arbetets titel – Title
Changes in peatland vegetation dynamics and their link to climate in a southern boreal bog during the last centuries

Oppiaine/Opintosuunta – Läroämne/Studieinriktning – Subject/Study track
Geology

Työn laji – Arbetets art – Level	Aika – Datum – Year	Sivumäärä – Sidoantal – Pages
Master's thesis	2020	53

Tiivistelmä – Referat – Abstract

Northern peatlands form a globally significant carbon reservoir holding almost one third of global terrestrial organic soil carbon. Peatlands are in constant interaction with the atmosphere and their carbon balance can change from a sink to a source. Climate is the one of the most important factors controlling peatland dynamics and subsequently carbon dynamics. As global warming is predicted to have increasingly strong impacts over the high latitudes, also peatlands will be affected. Peatlands are an environment defined by a certain type of vegetation, which can tolerate excess moisture and of often low pH. Peatland vegetation can be divided based on the preferred habitat conditions. Peatland vegetation compositions are not static, but instead everchanging and they react to changes in climate and environment, observed as shifts from vegetation assemblage to another.

I studied the climatic response of peatland vegetation compositions in Lakkasuo bog in Southern Finland. High resolution macrofossil approach was carried out to observe peat vegetation changes trough time, in particular I studied responses to known climate phases. To obtain robust chronologies, both ^{210}Pb and ^{14}C dating was applied. Peat bulk density and C/N ratio was also analysed, carbon accumulation rates calculated, and current vegetation and water table depth (WTD) measured in the field. Three peat sections, 50-60cm from the top, were analysed. Dating revealed that the peat sections reached back c. 300 years. Plant data was statistically analysed using Changepoint to make an objective core-to-core comparison of the changes and the timing of vegetation shifts.

Because WTD is largely defining the vegetation compositions in bogs, for Lakkasuo sites three bog microforms, i.e. microhabitats, currently representing different WTD levels were chosen for the palaeoecological analyses. Vegetation was inspected in high plant taxonomical level and as larger compositional groups (plant functional types). For changepoint analyses plant taxa were classified as "dry", "intermediate" and "wet" based on their preferred moisture conditions today.

Macrofossil data indicated clear shifts in vegetation composition in Lakkasuo as a response to the Little Ice Age (LIA) cool period and to current warming. LIA was characterised by presence of wet taxa. Current warming, in turn, is visible as an increase in dry taxa. This leads to the conclusion that climate has been the prevalent controlling factor for the bog vegetation during the last c. 300 years. Current development towards dry conditions in Lakkasuo will affect the peatland carbon dynamics. The peatland is projected to experience decrease in effective moisture hindering carbon uptake capability.

Avainsanat – Nyckelord – Keywords
boreal peatlands, climate change, environmental change, bog vegetation, plant macrofossil

Ohjaaja tai ohjaajat – Handledare – Supervisor or supervisors
Minna Väliranta
Eeva-Stiina Tuittila

Säilytyspaikka – Förvaringställe – Where deposited

Muita tietoja – Övriga uppgifter – Additional information

CONTENTS

1. INTRODUCTION

Northern peatlands contain a large stock of carbon and since the last deglaciation, i.e. during the last ca. 11 700 years, they have stored, through photosynthesis and incomplete decay processes, 436 Gt of atmospheric carbon (Yu, 2012; Loisel et al., 2014). Northern peatlands contain ca. 90% of the global peatland carbon pool making them the largest carbon reservoir in the biosphere (Yu, 2011) generating interest among scientist studying global change. In addition that peatland store carbon they also release carbon as carbon dioxide, CO_2, and methane, CH_4, emissions (Alm et al., 1999). As a very general rule wet fen peatlands emit large amounts of methane, while drier bogs are effective carbon sinks (Alm et al., 1999; Jouko Silvola et al., 1996). The effect of the on-going climate change is expected to be strongest in the northern latitudes and for instance precipitation is projected to increase drastically in the future but also periods of extreme drought are predicted to become more frequent (IPCC, 2013a). As northern peatlands are an essential part of the global carbon cycle it is important to understand the links between climate and peatland dynamics, including vegetation compositions, and subsequent further feedbacks and implications for carbon balance of peatlands.

Over their development history peatlands are affected by autogenic and allogenic forcing factors (Korhola, 1996; Tuittila et al., 2007). Besides autogenic forcing, i.e. natural time-dependent succession which results in vertical peat growth, peatlands are sensitive ecosystems which may reflect changes in environmental conditions, this is referred as allogenic forcing (Gorham, 1991). Due to allogenic factors a peatland may temporarily change from an effective carbon sink to a considerable carbon source (Waddington and Roulet, 1996; Mathijssen et al., 2016). Despite individual peatlands are very complex systems and local factors such as fires can override regional direct climate forcing, climate is one of the most important allogenic forcing factor which controls peatland dynamics and thus also peatland plant composition (e.g. Tuittila et al., 2007; Väliranta et al., 2017)

Moreover, peatland plant composition or plant functional types, which are strongly related to local hydrological conditions, largely determine carbon flux patterns (e.g. Tuittila et al., 2013). Because of these instrumental links between climate-driven hydrology and peatland vegetation, and plants and carbon dynamics, any information on past variations in vegetation may help us to understand response patterns of peatland

vegetation to climate variations and consequently allow us to reconstruct past carbon dynamics implications. Furthermore local habitat history is stored in situ in peat layers as plant macrofossils thus giving us an excellent record of the past ecological conditions, which again can be linked to known climate variations (e.g. Väliranta et al., 2007).

While the large-scale Holocene (the last ca. 11700 years) peatland dynamics patterns have been intensively studied in Finland (e.g. Korhola, 1992; Mäkilä, 1997; Mäkilä and Moisanen, 2007; Tuittila et al., 2007; Väliranta et al., 2012; Mathijssen et al., 2017), it is not yet completely resolved how fast peatland plant communities may respond to changes in environmental conditions. The aim of this study is to investigate more recent, i.e. the last centuries, changes in bog vegetation by using a high-resolution analysis approach. Climate reconstruction data (Tuittila et al., 2007; Väliranta et al., 2007; Mathijssen et al., 2016) and measured weather data are available for Finland, e.g. from Hyytiälä weather station used in this study.

2. PEATLANDS

Peatlands are by their geological definition soils that have deposited more than 30 cm thick organic layer, while in biology peatland is a habitat that contains peat accumulating vegetation (Laine et al., 2000). Though globally covering only ~3% of Earth's surface, peatlands account for almost one third of global soil carbon (Yu, 2011). Most of this carbon, ca. 90%, is stored in northern peatlands, which account for over 80% of global peatland area (Loisel et al., 2014). Peatlands are common in the Northern Hemisphere because of the suitable cool and humid climate. Annual precipitation of 200-1000 mm and mean temperature between 5°C and -12°C are required for peatlands (Yu et al., 2009). Peatlands formed and expanded in great extend after glaciers retreat in warming Holocene climate when suitable environmental conditions prevailed (Ruppel et al., 2013).

Peat is a product of incomplete decomposition under anoxic conditions. Peat forms from the plants growing *in situ* and therefore it represents local environment. Peat can accumulate even thousands of years when it creates a palaeoecological archive and its stratigraphy is an excellent way to look at past changes (Gorham, 1991; Mauquoy and van Geel, 2007). Traditionally, peat stratigraphy has been used for climate reconstructions and the main events during the last millennium, for example, are visible in the peat records

around the northern hemisphere as dry or wet periods (Charman, 2002; Väliranta et al., 2007; Charman et al., 2013; Mathijssen et al., 2016).

The peat profile can be divided into two layers based on oxygen availability. Acrotelm is the drier surface layer and catotelm is the permanently waterlogged layer (Ingram, 1978). Around 30-80% of plant material is decomposed in the oxic acrotelm (Malmer and Wallén, 2004). The rest is buried in anoxic conditions in the catotelm, where rates of decay are two or three orders of magnitude lower (Clymo, 1984). Thicker oxic layer means higher decomposition (Riutta et al., 2007). Thus, most of the carbon balance of peatlands is determined by processes of carbon intake from plant matter and the loss of carbon in decaying in acrotelm (Malmer and Wallén, 2004). Microbial communities responsible for breaking down plant material change depending on depth in the peat column (Song et al., 2016).

Peatlands are divided roughly into minerotrophic fens and ombrotrophic bogs. Bogs are a type of peatland which are nutrient poor getting all their fresh water from rainfall, compared to fens, which have nutrient-rich waters from the surrounding and from the groundwater. Ombrotrophication is the succession of a northern peatland from a more nutrient rich fen to a poorer bog. Also known as fen-bog transition, it can be clearly detected in macrofossil analyses (e.g. Loisel and Yu, 2013a; Ronkainen et al., 2014; Väliranta et al., 2017). Fen-bog transition can be initiated by a change in hydrology (Tahvanainen, 2011) and final ombrotrophic bog receives nutrients only from rainfall as surface peat layer become separated from groundwater. Typically a slow process, ombrotophication can be accelerated by disruption (Kuhry, 1994; Väliranta et al., 2017). Due to accumulation and growth, peat forms a thickening blanket leading to changes in the hydrology and vegetation through time.

2.1. Bog vegetation

For vegetation, bogs provide a unique and harsh environment with low pH (often <4), electrolyte and calcium. Typical vegetation is mosses (*Bryophyta)* and certain vascular plants, mainly shrubs. For mosses, most important is the genus *Sphagnum*, while other mosses found are sparser but significant in certain environments. For vascular plants especially important are the taxon *Eriophorum vaginatum* and some species of the genus *Carex*, but other herbaceous plants are also found commonly, e.g. *Scheuchzeria palustris*.

Sphagnum mosses are usually extremely abundant in peatlands and they can cover even up to 100% of peatland surface (Gunnarsson, 2005; Rydin and Jeglum, 2006). It is estimated, that in relation to carbon storage *Sphagnum* is the most important genus in the world (Clymo and Hayward, 1982) increasing peat formation and carbon sequestration of peatlands (Loisel and Yu, 2013a). In the ca. 380 species of *Sphagnum*, some 50 species are globally important peat producers (Gunnarsson, 2005) being most common constituent of peat and more resistant to degradation compared to most vascular plants (Mauquoy and van Geel, 2007). *Sphagnum* species have a wide range of habitats inside peatlands, as they have adapted to varying conditions from wet to dry and open to wooded areas (Rydin and Jeglum, 2006). *Sphagnum* can themselves initiate a change within peatland towards more acidic and bog-like environment (Granath et al., 2010).

Vegetation in bogs forms so-called microforms following water table depth (WTD) of peatland with plants that are specialised in different microhabitats controlled by moisture conditions. Bogs microforms are hollows (wet), hummocks (dry) and lawns (intermediate) and all habitats can be further divided into for instance low or high lawn. Hollows are surfaces very close to (0-5 cm) the water table or they are inundated, and so their species composition consist of species that can survive in the wet conditions. Hummock WTD is typically 20-35 cm below peat surface and inhabited by the dry-specialised species. These may include shrubs and trees as well as many distinctive dry *Sphagnum* taxa, such as *S. fuscum*. For lawns taxa from both ends of the hydrological gradient can be found supplemented by taxa whose preferred niche is intermediate WTD. Microhabitats are characterized by special functional traits, e.g. *Sphagnum* species growing on hummocks have higher capillarity, which retains moisture (Rydin and Jeglum, 2006).

Vegetation changes reflecting the microforms and their WTD in one bog may be greater than between the bogs inside spatially large area (Waddington and Roulet, 2000; Juottonen et al., 2015). Bog vegetation is not static, and the shift from microform to another is caused by changes in water table, which in turn can be influenced by a number of factors, e.g. drainage or environmental change (Mcmullen et al., 2004). Vegetation changes in bogs may be slower when related to for instance autogenic ombrotrophication but also quite fast (Tahvanainen, 2011). Depending on scale, different factors are

controlling peatland vegetation: climate is a global scale factor, on the other hand, local factors can be in short term much more impactful (Tuittila et al., 2007).

Net primary production (NPP) is the bulk amount of production a vegetation community is responsible for. NPP controls ecological processes responsible for carbon dynamics of terrestrial ecosystems (Vitt et al., 2001; Gunnarsson, 2005). The primary production in bogs is determined by vegetation composition. NPP can vary greatly within a peatland (Vitt et al., 2001) as the nutrient availability and productivity vary across microforms. Species more common in hummocks, e.g. *Sphagnum fuscum*, have lower productivity than species growing in more eutrophic microhabitats, e.g. *S. fallax* (Gunnarsson, 2005). The difference between NPP and decomposition is stored as carbon in plant litter in peat (Clymo, 1984).

2.2. Past climate variations

Northern peatlands are strongly connected to the climate. As they store huge amounts of carbon and cover vast areas of land, their role in global biogeochemical cycle should be carefully examined. Northern peatlands have developed in a varying climatic condition characterised by successive colder and warmer periods as throughout Holocene climate history, fluctuations of climate have been characteristic for Holocene period (e.g. Bradley, 2014; Anchukaitis et al., 2017). The role of Holocene climatic periods in the context of peatland growth and development is relatively well understood (e.g. Korhola et al., 2010; Loisel and Yu, 2013a; Ruppel et al., 2013).

Since the Last Glacial Maximum (LGM) circa 21 ka BP, glaciers have retreated in the Northern hemisphere to their current extent and peatlands have spread into new areas in northern latitudes (Yu, 2011; Ruppel et al., 2013). The retreat has been slower at times and glaciers have also stopped melting and even advanced. The most significant period of cooling during this period is the Younger Dryas (YD) 12. 5-11.7 ka BP (Fairbanks, 1989), although recent modelling studies suggest warm summers also for YD (Schenk et al., 2018). Summer warming continued after the YD (Väliranta et al., 2015), and winter temperatures reached the warmest values during Holocene Thermal Maximum (HTM) around 8-5 ka BP (Renssen et al., 2009). During HTM climate was beneficial for vegetation growth and globally accumulated peat, thus carbon, rapidly (Yu et al., 2009).

The climate in the Northern hemisphere has undergone few anomalous climatic periods during the last millennium. Warmer period between ca. 1000-1580 was known as the Medieval Climate Anomaly (MCA) (Diaz et al., 2011), and the Little Ice Age (LIA) was a period of cooler climate between 1580-1880 (Mann et al., 2009; Diaz et al., 2011; Linderholm et al., 2018). Overall the warming trend since LGM continued. After the end of LIA, global climate started to warm with an increasing intensity (Anchukaitis et al., 2017; Linderholm et al., 2018). For the last 150 years, warming has been going on with an accelerating pace with some cooler periods in between (Goosse et al., 2006). This pattern reflects rising concentrations of greenhouse gases (GHG), namely CO_2 and CH_4, caused by human activity (Crowley, 2000). In Finland anthropogenic rise of temperature since the industrialization is over 2°C (Mikkonen et al., 2015). Since the 1980's the warming in Finland is clearly perceived in weather data (Finnish Meterological Institute, 2020).

2.3. Peatlands and the climate change

Peatlands occupy various pH and nutrient niches or hydrological settings (Malmer and Wallén, 2004; Rydin and Jeglum, 2006). Changes in environmental conditions will however cause changes in peatland ecosystems when they respond to local water regime shifts (Linderholm et al., 2018; Swindles et al., 2019). Peatlands in northern latitudes, bogs and fens, are reacting to a warming climate and hydrological changes in individualistic ways (Kokkonen et al., 2019; Riutta et al., 2020). Current warming causes rise in evapotranspiration rates due to increase in surface temperature and changes in precipitation patters (Westra et al., 2014; Radu and Duval, 2018) leading to drying of peatlands (Swindles et al., 2019). Changes in precipitation are more local in nature than temperature and therefore predicting is challenging (IPCC, 2013b).

Peatlands are projected to fix more carbon as warming climate increases the amount of photosynthesis (Walker et al., 2015; Gallego-Sala et al., 2018). However, recent increase in nitrogen supply and dryness (Swindles et al., 2019) has potential to lower the carbon accumulation in peatlands (Malmer and Wallén, 2004; Zhang et al., 2020). Drying will shift vegetation towards woody species (e.g. Strack et al., 2006) which have entirely different carbon dynamics than open fens and bogs. Droughts and floods are also expected to be more common (e.g. IPCC, 2013b; Westra et al., 2014; Cook et al., 2015). They affect the hydrology of a peatland and thus vegetation. The surface wetness in peatlands

is determined by the precipitation-evaporation balance. Predicted changes in precipitations can cause droughts that lead to drying of peatlands making fires more common (Turetsky et al., 2011). Fires have played major role over the development history of the peatlands throughout the Holocene affecting their dynamics and consequently carbon intake (e.g. Kuhry, 1994; Sillasoo et al., 2011; Morris et al., 2015).

2.4. Peatland carbon dynamics

Carbon is stored in peat via burial of incompetently decaying plant matter and released back into the atmosphere by microbial metabolism and plant respiration (Laine et al., 2009). Approximately 5% of carbon within plants is transferred into peat (e.g. Tolonen and Turunen, 1996; Vitt et al., 2001). Peatlands are commonly sinks for atmospheric carbon, but can turn into sources as well (Saarnio et al., 2007). More specifically, they often are sinks for carbon dioxide and sources for methane. However, this can be subject to change. For example, drainage of peatlands can switch these dynamics (Minkkinen et al., 1999). Methane particularly is important, for it is a potent greenhouse gas and it is emitted, possibly in large volumes, from peatlands (Korhola et al., 2010) making peatlands the largest natural source of methane (Turetsky et al., 2014). While storing large amounts of carbon, the expansion of peatlands has increased the atmospheric CH_4 during Holocene (Blunier et al., 1995). In long term, peatlands will turn into carbon sinks effectively sequestering carbon (Mathijssen et al., 2016, 2017).

While plant matter is getting buried and decomposed carbon flux is mostly going through atmosphere (Gorham, 1991) and most of the carbon in peatlands is rereleased annually back to atmosphere (Vasander, 1982; Silvola et al., 1996). Methane is produced by anaerobic decomposition of peat plant matter (Gorham, 1991). As a potent greenhouse gas, methane's role in peatlands is vital to understand. It is produced in the anoxic layer and becomes oxidised when it is transported through overlying oxic layer. In hummocks, aerobic peat layer is thicker than on wetter surfaces where anoxic conditions prevail closer to the surface. In inundated wet hollows where the water table is overlying vegetation microbes have no time to consume methane (Merilä et al., 2006; Juottonen et al., 2015).

Generally, the net result of CO_2 uptake and CH_4 emissions is the overall radiative forcing (RF) of peatlands (Frolking and Roulet, 2007; Mathijssen et al., 2017) and plants have specific role in CO_2 and CH_4 fluxes as well as rates of production and decay, e.g. hollows

have higher CH_4 emissions than hummocks (e.g. Alm et al., 1999; Riutta et al., 2007). Peatlands form long term negative climate feedback but may become short-term positive feedback (Gorham, 1991; Frolking and Roulet, 2007). Vegetation composition affects the decomposition of peat together with abiotic factors, e.g. oxygen-availability and temperature (Mäkilä and Goslar, 2008). Microhabitats even in close proximity can be different in their carbon balance (Waddington and Roulet, 2000). Generally, bog species are more efficient at sequestrating carbon than minerotrophic species (Granath et al., 2010) and CH_4 emissions are smaller (Turetsky et al., 2014).

The changes in peatland dynamics in Holocene show how peatlands role in global carbon sequestration varies. Peatlands have been a carbon sink overall, while CH_4 emissions have fluctuated more (MacDonald et al., 2006; Yu et al., 2009; Korhola et al., 2010). Methane flux is strongly linked to total peatland area and during times of rapid peatland expansion methane emissions have increased (Yu, 2011; Yu et al., 2013). Current accelerating warming has been found to increase carbon accumulation in peatlands (Loisel and Yu, 2013a). However, increased microbial activity and decomposition of peat or drying of peatland surface may hinder the positive effect of increasing carbon sequestration (Dorrepaal et al., 2009; Gill et al., 2017; Swindles et al., 2019).

To better understand the dynamics and associated changes of peatland vegetation as a to climate, I apply high-resolution macrofossil analyses to peat cores collected from Lakkasuo, a boreal bog in Southern Finland. I link past changes in plant compositions to climate data using meteorological measurements from a nearby research station and palaeo-based reconstructions. Especially centennial to decadal scale changes in peatland vegetation dynamics are less well documented and my thesis is targeting to provide useful insights for these more poorly understood timescales. In this study I focus on past changes in vegetation and associated changes in hydrological conditions. I also investigate if statistical changepoint analysis tool is useful in investigating peat macrofossil data as linked to climate data. My research hypothesis is: Climate variations have resulted in changes in bog plant species compositions and these data can be used to predict future peatland dynamics under changing climate.

3. MATERIALS AND METHODS

3.1. Study site

Lakkasuo (61°48’ N, 24°19’ E, 150m a.s.l.) is an eccentric raised bog with a total area of 1.2km^2. It is located in Southern Finland in Orivesi (Fig. 1) in the southern boreal zone. The mean annual temperature is 3.1℃, with mean July temperature 15.3℃ and January -8.9℃ (1960-1990). Annual rainfall is around 700mm. Lakkasuo has been intensively studied over decades, owing to its proximity to the Hyytiälä Research Station, which enables easy access. Thus, palaeoecological and ecological data are readily available. Lakkasuo has a mosaic of microhabitats with pristine part while some of the margins have been drained (Laine et al., 2004). Local weather data from the Juupajoki-Hyytiälä research station allows linking the changes in vegetation to weather conditions.

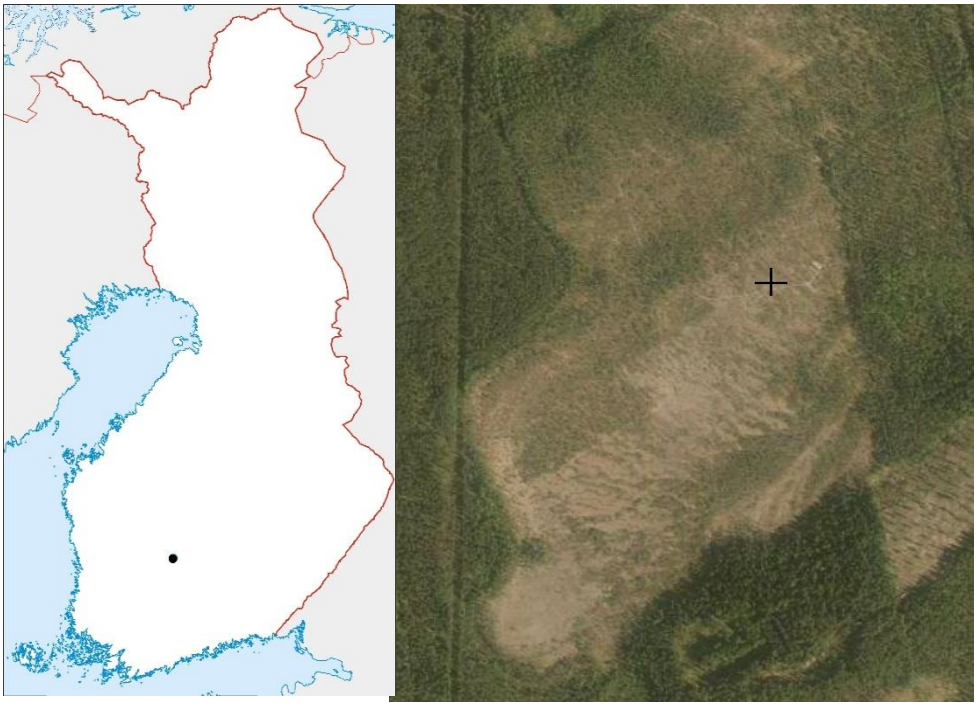


Figure 1. Lakkasuo location (.) and the site of core collection (+) in aerial photograph (photos from Maanmittauslaitos).

Core collection was carried out in October of 2016. Coring points were selected on the pristine part of the bog to minimalize the effect of forestry and other anthropogenic factors. The top ~60 cm was collected using a box corer (Fig. 2). Three cores were retrieved, and the coring points represent low lawn (LL), high lawn (HL) and hummock (H) habitats which are considered most responsive to hydrological changes. Hummock habitat core was retrieved from the low hummock subtype, which closer to the WTD than

another hummock habitat, high hummock. Vegetation was determined around the coring point and water table measured from the sampling hole down from peat surface.

After sampling, the peat cores were transported to univ

ersity where they were frozen and studied. First a visual examination of the cores was made, and misplaced peat material was carefully removed. Next the cores were cut into 1 cm subsamples for further analysis. All work was done carefully with specific equipment that was rinsed after every subsample to prevent contamination. Part of the subsamples were stored in a refrigerator for macrofossil analysis, and part was freeze-dried and ground for C/N analysis and ^{210}Pb-dating purposes. For bulk density calculations, subsamples of 5 cm^3 were dried and weighted.

Figure 2. Fresh sample core, ready to be wrapped in plastic. © S. Piilo

3.2. Methods

3.2.1. Plant macrofossil analysis

A high-resolution plant macrofossil analyses was performed out following the Quadrant and leaf protocol (QLC) by Mauquoy and van Geel (2007), modified by Väliranta et al. (2007) for three cores. Subsample size was 5 cm^3 and these were sieved gently under running water using a 140-µm sieve. From the remaining material all plant macrofossils were identified using a stereomicroscope. For more accurate species-level identification a high-power light microscope was used. The resolution was 2 cm, expect for the topmost

15 cm of Lakkasuo hummock, where resolution was 1 cm. The amount of most abundant species was estimated in percentages (%), while for instance seeds were counted individually. A total of 93 samples from Lakkasuo were analysed.

3.2.2. Bulk density and C/N analyses

Bulk density for the peat profiles were calculated in 1 cm resolution by drying and weighting 5 cm^3 of peat. Bulk density is calculated using simple formula, $\rho = M/V$, where ρ is dry bulk density, M is mass of soil and V is total volume.

For sample cores, carbon-nitrogen ratio (C/N) was measured every four centimetres to investigate carbon and nitrogen content. C/N was analysed using Micro Cube Elemental Vario CNS-analyser in the laboratory of department of geosciences and geography, University of Helsinki. C/N ratio can also indicate differences in vegetation compositions throughout peat profile as the ratio changes depending on vegetation. Typically, *Sphagnum* bogs have higher C/N ratios than other peatlands (Loisel et al., 2014).

3.2.3. Dating

Analysed peat cores were dated to obtain precise chronologies. Two dating methods were used to minimize margin of error and to obtain best possible age-depth models. For the topmost peat ^{210}Pb-dating was applied. I personally carried out ^{210}Pb laboratory processes in University of Exeter, United Kingdom. Method is based on the decay chain of ^{238}U and the occurrence of radioactive ^{210}Pb that is generated in the atmosphere and accumulated everywhere in nature. The stable end product of the chain is ^{206}Pb. Lead ^{210}Pb-dating method is ideal for analysing organic material (Sanderson, 2013). Dating was done following Sanderson's (2013) description of alpha (α) radiometric dating.

Analysis was done with precision and care. Freeze-dried peat subsamples were spiked with a known radioactive source of ^{209}Po to enhance the signal of ^{210}Pb. Sample dissolution was done with 10 ml of nitric acid HNO_3 and acid digestion using 10 ml of 30% hydrogen peroxide H_2O_2. Next the samples were repetitively boiling with 5 ml of 6M hydrogen chloride HCl. After moving the remaining material to test tubes, they were centrifuged in 2500 rpm for 10 minutes. The solution was then placed in acid washed jars and filled with ascorbic acid. Small silver discs with one side painted and with small holes were suspended in jars using fishing line. After 24 hours of mixing on magnetic stirring tables, the silver discs were rinsed and placed in an alfa counter for three days.

Lead ^{210}Pb-dating provides a continuous chronology over the past ca. 150 years. For the older peat layers radiocarbon dating was also applied. ^{14}C dating is based on the known decay rates of carbon 14 isotope. Radiocarbon is stored in plants trough photosynthesis until the plant dies after which carbon starts to decay in plant matter. With a half-life of 5730 ± 40 years, ^{14}C is more suitable for samples older than 300 years, up to 50000 years (Taylor, 2000). ^{14}C dating for bottom of the Lakkasuo H, HL and LL cores was done in in the Poznan Radiocarbon Laboratory, Poland.

3.2.4 Changepoint analyses

I used R package 'changepoint' to find changes in time series (Killick, 2014). Changepoint analysis was carried out for all plant macrofossil data, peat and carbon accumulation rates of HL and H cores and Hyytiälä weather data to statistically infer changes in datasets. Function cpt.mean was used for macrofossil and weather data and cpt.meanvar for accumulation rates. Methods "At Most One Change" and "Pruned Exact Linear Time" were used depending on if one or more changes were looked for in a timeline. Changepoint analysis was done against time except for the LL macrofossil data, for which changepoints were plotted against depth.

4. RESULTS

4.1. ^{14}C and ^{210}Pb chronologies

^{14}C results provide basal dates for each of the three cores (Table 1). The age ranges were relatively large, but basal ages of all cores seem to be around 1700 AD. Results of ^{210}Pb analysis provide a continuous chronology through the H and HL cores (Fig. 3 and 4). This is vital to connect acquired macrofossil data to historical changes in climate. Plotted against depth, lead 210 results yield estimates of peat accumulation. Curve slopes show that accumulation has increased closer to modern times. Accumulation has especially high been during the 21st century in both cores. Similarly, in both cores accumulation slows down further down the core and in HL a steep drop in accumulation occurs at 32 cm in 1924 AD. In H, the decline in accumulation is much steadier. For the LL core only radiocarbon dating was applied, while and not lead 210 chronology is not available.

Table 1. ^{14}C dating results for Lakkasuo Low Lawn, Hummock and High Lawn.

Sample ID	Radicarbon age BP	2 σ calibrated age ranges	Calibration curve
LAK LL	180 ± 30 BP	95.4% probability 1652AD (19.1%) 1696AD 1726AD (51.9%) 1814AD 1836AD (4.1%) 1877AD 1916AD (20.4%) ...	IntCal 13
LAK H	70 ± 30 BP	95.4% probability 1690AD (24.3%) 1730AD 1810AD (71.1%) 1924AD	IntCal 13
LAK HL	60 ± 30 BP	95.4% probability 1692AD (23.1%) 1728AD 1811AD (72.3%) 1920AD	IntCal 13

4.2. Age-depth models

Lead 210 and radiocarbon dating results were combined with R-software Bacon to produce age-depth models for H and HL (Fig 5). Accumulation rates can be interpreted from the models: steeper curve suggests higher rate of accumulation. In both sites, higher accumulation rates are reached in the top part, i.e. more recently. Respective bottom mean ages for HL is c. 256 cal BP (1694 AD) and for H 227 cal BP (1723 AD). Both cores have generally similar pattern, with accumulation increasing towards the current times and at around 0 cal BP (1950 AD) accumulation rises. The HL, 'Lawn', core shows slightly higher accumulation rates in top. Error margins on the models are small in the top part, but error grows significantly in the deepest lead samples. The ^{14}C dates at the bottom of cores show a very large age ranges, therefore data below the lead dates, which reach to c. 35 cm and are more accurate, should be interpreted with care.

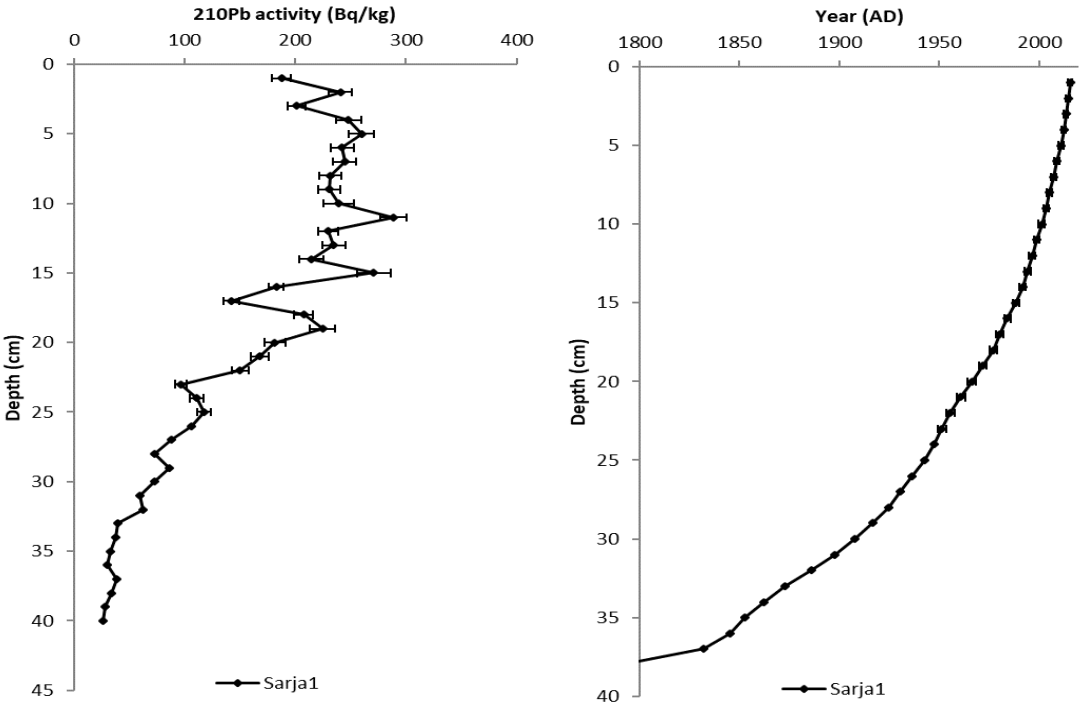


Figure 3. Lakkasuo H 210Pb results. Left. 210activity as Bq/kg and right: dating curve, years shown in Anno Domini.

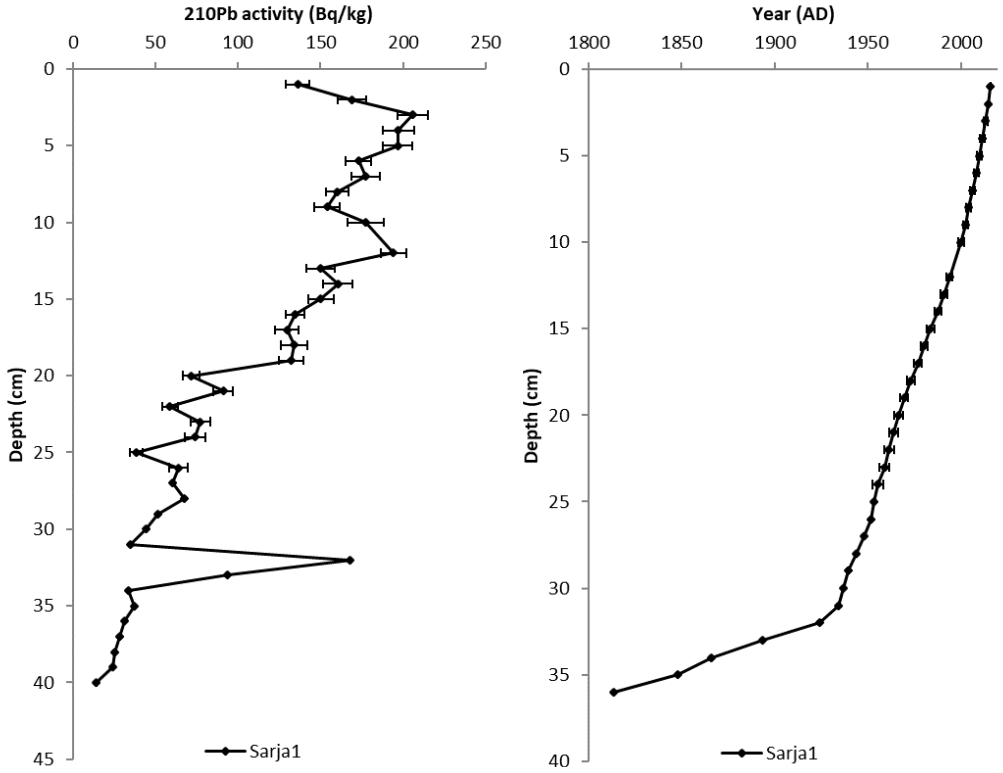


Figure 4. Lakkasuo HL 210Pb results. Left: 210activity as Bq/kg and right: dating curve, years shown in Anno Domini.

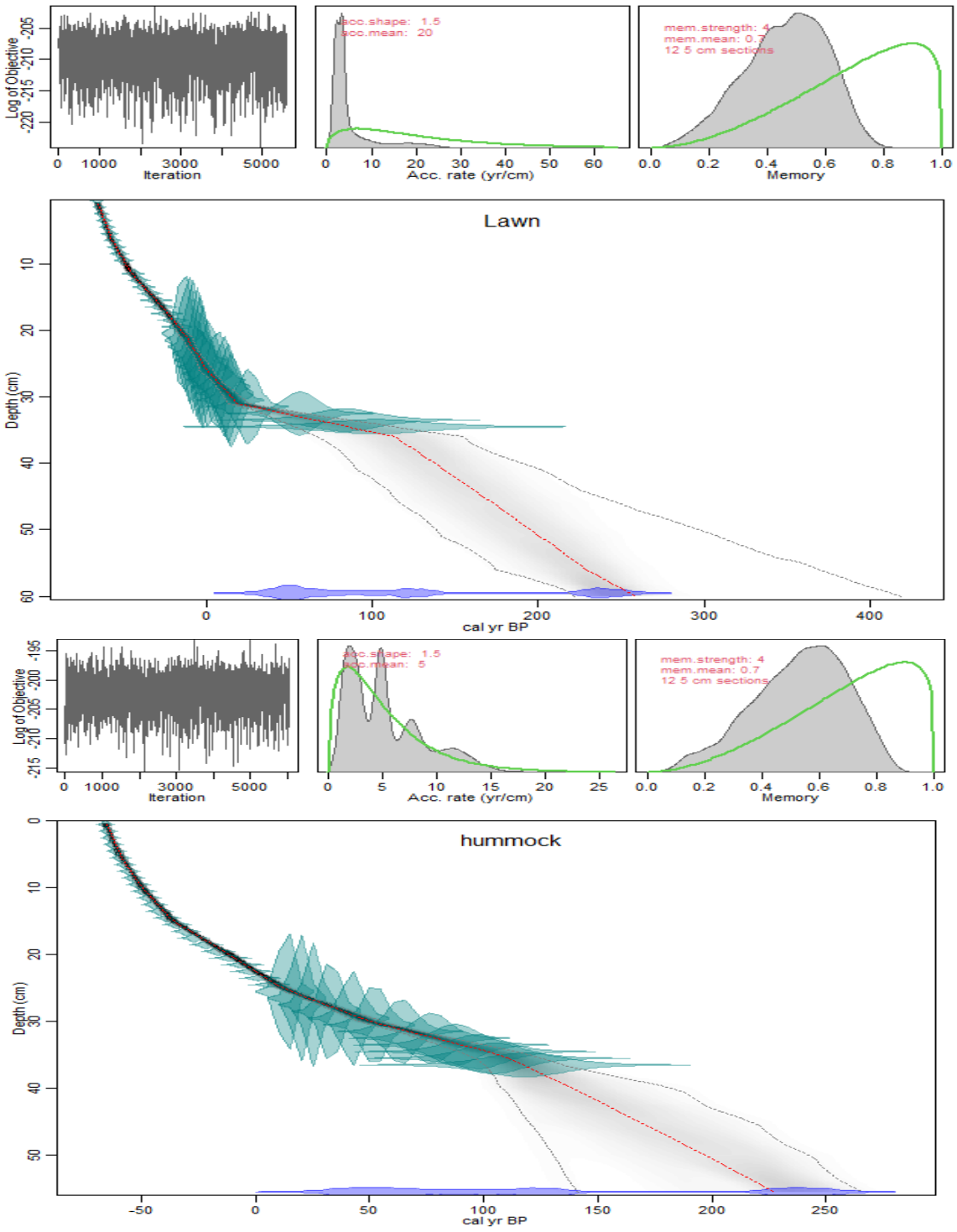


Figure 5. Lakkasuo HL (top) and H (bottom) age-depth model graphs. Lead dates are shown in green and carbon dates from the bottom of the cores in blue. Grey area indicates the probability range of the model, dotted grey lines are the 95% confidence intervals and red line shows the weighted mean age-depth model. In the top pictures Markov Chain Monte Carlo iteration, accumulation rate that estimates accumulation rates and "memory" of accumulation rate are shown.

4.3. Plant macrofossil analyses results

All three Lakkasuo cores representing three different microforms contain variable current vegetation and also macrofossil compositions distinctive to each microform. Taxa more indicative to wet habitat are found more abundant in low lawn core, where the peat surface is closest to the WTD and dry-resistant taxa are in turn found in hummock, where WTD is beneath thicker peat layer. In the intermediate high lawn, taxa from both ends are found. Current *Sphagnum* cover was dominated by *S. fuscum, S. balticum* and *S. rubellum* for hummock (H), high lawn (HL) and low lawn (LL) samples respectively (Table 2). The proximity and similarities between HL and LL habitats are apparent in current vegetation. The proportions of *S. rubellum* and *S. balticum* varied greatly within Lakkasuo lawns, and the distinction between low and high lawn was made based on WTD. The difference between HL and LL is also underlined by species related to dry and wet conditions, i.e. *S. fuscum* and *Scheuchzeria palustris* respectively.

Table 2. Vegetation and WTD of the sampling plots during sampling in 2016. Moss cover was first estimated, and the rest of the plants were counted by leaf area cover. Values are percentages (%) of cover.

	Hummock	**High lawn**	**Low lawn**
Sphagnum fuscum	75	8	
S. rubellum		5	90
S. balticum	20	85	9
Mylia anomalia	1		
Eriophorum vaginatum	30	3	8
Aandromeda polifolia	6	2	2
Empetrum nigrum	2		
Rubus chamaemorus	2		
Vaccinium oxycoccos	2	2	1
Scheuchzeria palustris			1
WTD	7 cm	5 cm	3 cm

Hummock section (Fig. 6) was 56 cm long. At the bottom *Sphagnum* section *Sphagnum* was dominant. However, immediately at 54 cm it declined rapidly and completely disappeared by 46 cm. *S.* sect. *Sphagnum* was replaced by *S. balticum and S. majus*, with *S. majus* being present only between 54-52 cm. *S. balticum* was the prevalent moss between 54-48 cm and remained constantly present throughout the section. Together with water-tolerant *Sphagnum* taxa some vascular plants indicating wetter conditions

appeared, e.g. *Equisetum* remains, which were found at depths 48 cm, 52 cm and 54 cm. At the depth 48 cm *S. fuscum* became the dominant taxon and remained dominant until the surface. Other *Sphagnum* taxa diminished and were found only in small percentages or, as in the case of *S. rubellum* at 20 cm, short-lived in the section. *E. vaginatum* was present throughout the section, being very abundant at depths 36-30 cm and notable *Carex* remains were found at depths between 30-12 cm. Some wood remains were also found after the depth 20 cm. Between 16 cm and surface Ericaceous and *A. polifolia* remains were common indicating peat surface environment and vegetation cover very similar to the current. Only non-*Sphagnum Bryophyta*, *Mylia Anomalia* was present with *S. fuscum* until 10 cm and after appeared few times deeper in the section.

High Lawn section (Fig. 7) was 60 cm long. Bottom sample at 60 cm was almost entirely *S.* sect. *Sphagnum*. At all other depths, excluding 46 cm, *S. balticum* dominated steadily. Between 58 cm and 22 cm together with *S. balticum S.* sect *cuspidata* and *S. angustifolium* formed the moss cover. Sect. *cuspidata* had a slow and steady drop in abundance between 58 cm and 20 cm with an extremely strong peak at 46 cm. Similarly, *E. vaginatum* was found quite steadily between 60 cm and 20 cm. Also, vascular plants indicative of wet habitat are found before 20 cm, e.g. *Carex* sp. and *Scheuchzeria palustris.* At 20 cm a clear shift in vegetation is found with the disappearance of *S. angustifolium* coinciding with the appearance of *S. fuscum*. After 20 cm *S. fuscum* was present at the top part of the section, most prominent at 7 cm. Interestingly S. *fuscum* was rare at the surface but appeared more at 2 cm. Together with S. *fuscum* ericaceous and *A. polifolia* remains were most common above 20 cm while also discontinuously appearing further down in the section.

Low lawn section (Fig. 8) was 45 cm long. At the bottom of the section, between 40-45 cm *S.* sect. *Sphagnum* was the dominating *Sphagnum*. Between 39 cm and 32 cm peat was very humified with some unidentified organic matter (UOM). Also, *Carex* appears before 30 cm indicating clearly different habitat to that above. Before 30 cm *Sphagna* that prevail in wetter environments are abundant, namely *S. balticum* and *S. cuspidatum* (sect. *cuspidata*). *S. balticum* is present in every subsample, while *S. cuspidatum* only appears briefly but abundantly in few centimetres. *S. angustifolium* was found in small amounts at 37-13 cm. Between 30 cm and surface *S. rubellum* dominates the LL section while *E. vaginatum* is relatively abundant.

Macrofossil analysis shows how only few taxa dominate the bog peat cores. At all sections and depths, *Sphagna* was the most abundant species and *Sphagnum* sect. *acutifolia* (*S. fuscum* and *S. rubellum*) are extremely dominant in many points in H and LL, while *S. balticum* characterizes most of the HL. The LL habitat was most variable in *Sphagna* composition. At the bottom of each core *Sphagnum* sect. *Sphagnum*, especially *S. medium* (syn. *S. magellanicum*), was the dominating taxa before abruptly disappearing. Vascular plants were overall sparsely detected, only *E. vaginatum* was found often and was even typical at some depths, while *Carex* was generally only found in small amounts at certain depths. Many other taxa were found as single or few individuals, and these are not discussed further. Additionally, few small pieces of charcoal were found, but not enough to suggest a local fire event.

4.4. Peat properties

In bulk density, cores showed a declining trend towards the top (Fig. 9). At bottom of the core densities were 0,0639 g/cm^3 for H, 0,04564 g/cm^3 for HL and 0,04956 g/cm^3 for LL at the surface bulk 0,06198 g/cm^3 for H, 0,02968 g/cm^3 for HL and 0,03404 g/cm^3 for LL and. Between the bottom and surface, bulk densities varied, and changes were sometimes abrupt showing some prominent peaks in densities along the core. Clear peaks were at depths 54 cm and 15 cm in H and at 43 cm in LL. Typically, bulk density values tend to increase in peat as the depth increases due to compression and breakdown of material. In each core, density values increase sharply above the deepest subsamples. C/N values for the cores show a slight upward trend between bottom and surface (Fig. 10). In HL and LL cores, notable peaks in C/N can are in HL peaks at 37 cm and 33 cm and in LL at bottom, at 25 cm and at surface. H samples see a steadier rise in C/N towards the top with a sharp drop at the lowest subsample at 57 cm.

Peat accumulation rates and apparent carbon accumulation rates were calculated for the dated HL and H. Carbon accumulation was calculated for each cm separately by multiplying peat accumulation rate with bulk density and carbon content. In H mean peat accumulation was 2,83 mm yr^{-1} over the studied time period and mean carbon accumulation was 110,5 g(C) m^{-2} yr^{-1}. In HL similarly 0,30 mm yr^{-1} and 71,5 g(C) m^{-2} yr^{-1} (Fig. 11). Maximum values of carbon accumulation were 306,5 g(C) m^{-2} yr^{-1} in H and 201,1 g(C) m^{-2} yr^{-1} in HL, at depth 2 cm in both cores. Generally, H has accumulated more carbon than HL.

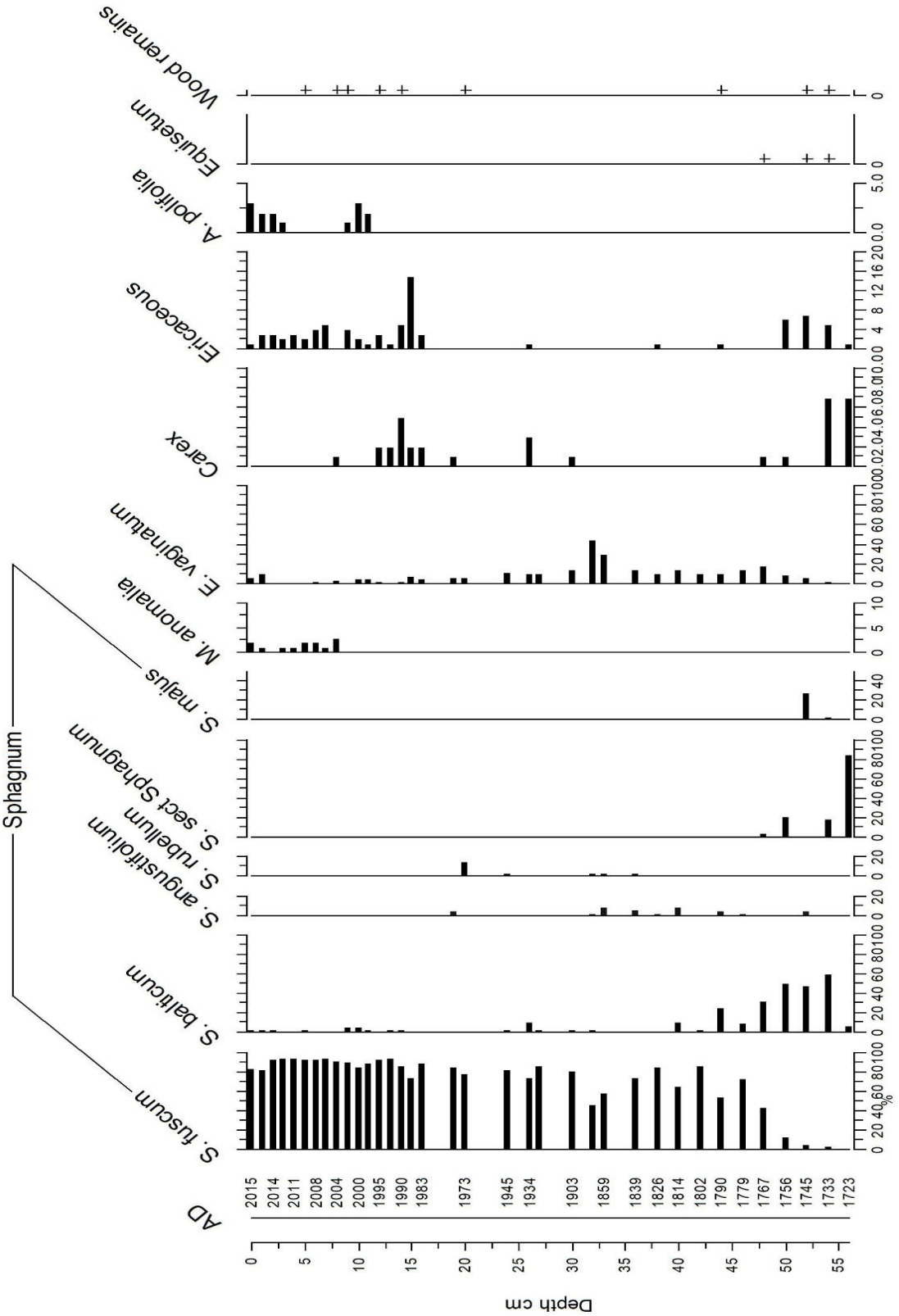


Fig 6. H plant macrofossil data. Values as percentages (%), (+) indicates single or few identified remains. Only selected taxa are shown.

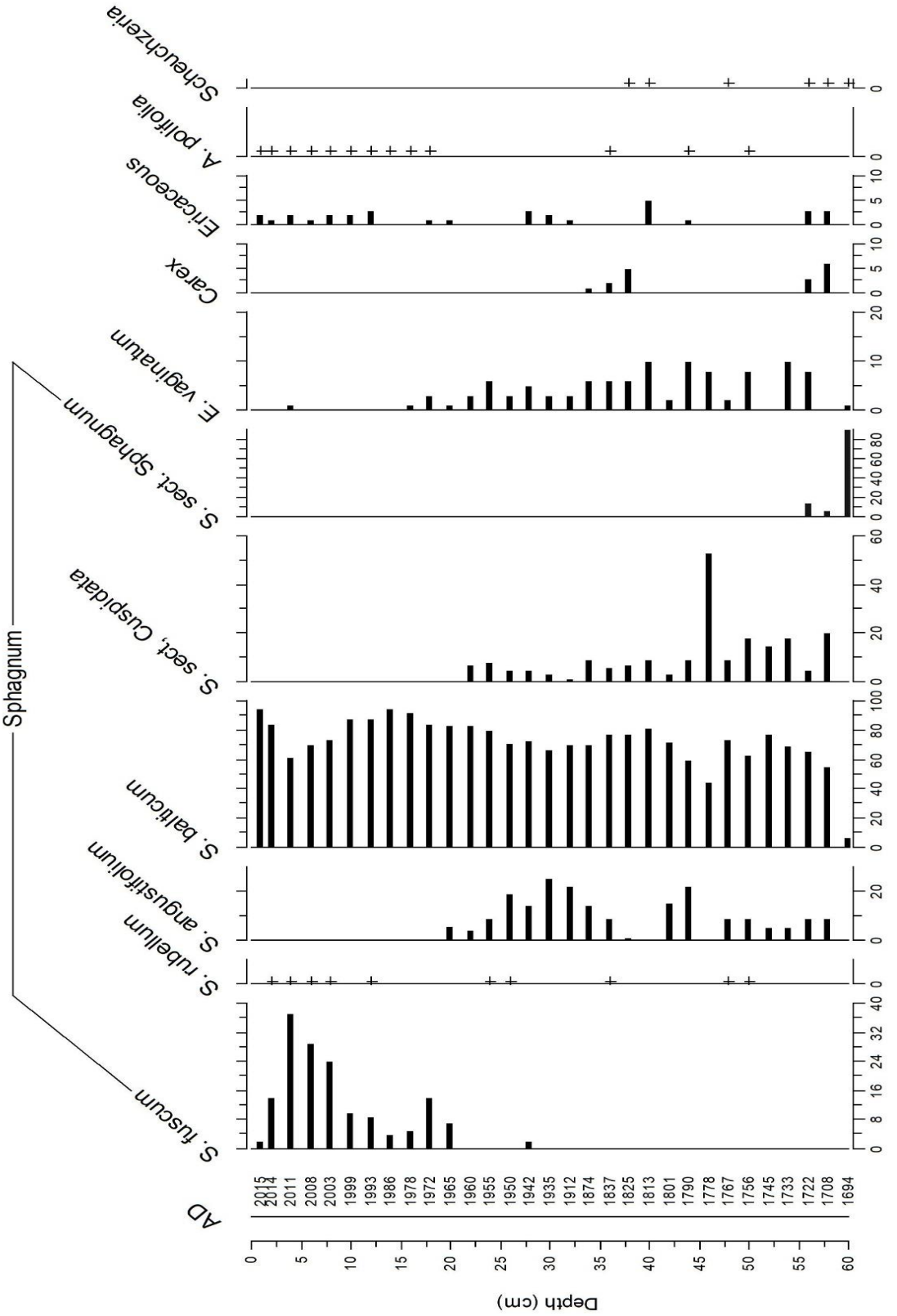


Fig 7. HL plant macrofossil data. Values as percentages (%), (+) indicates single or few identified remains. Only selected taxa are shown.

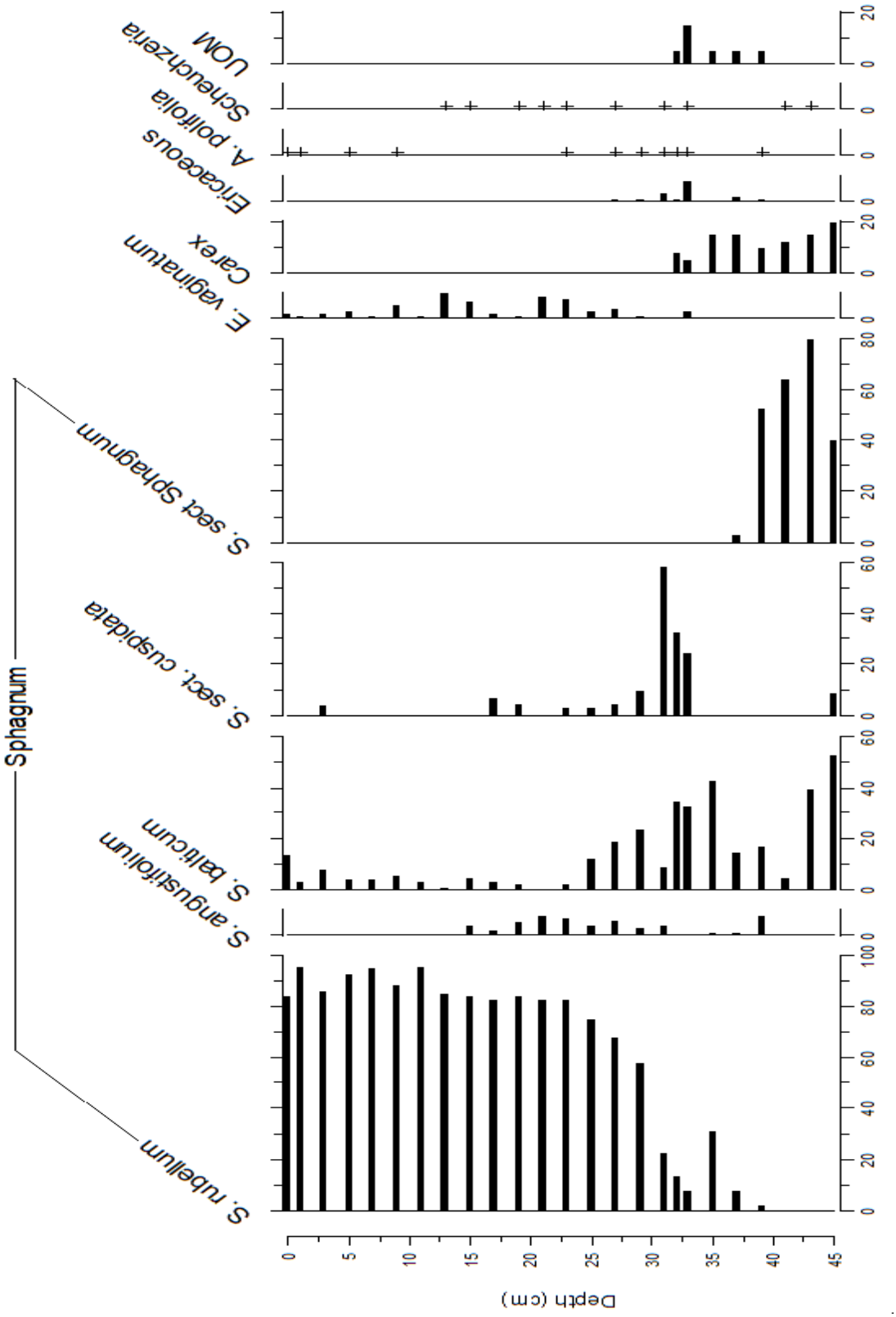


Fig 8. LL plant macrofossil data. Values as percentages (%), (+) indicates single or few identified remains. Only selected taxa are shown.

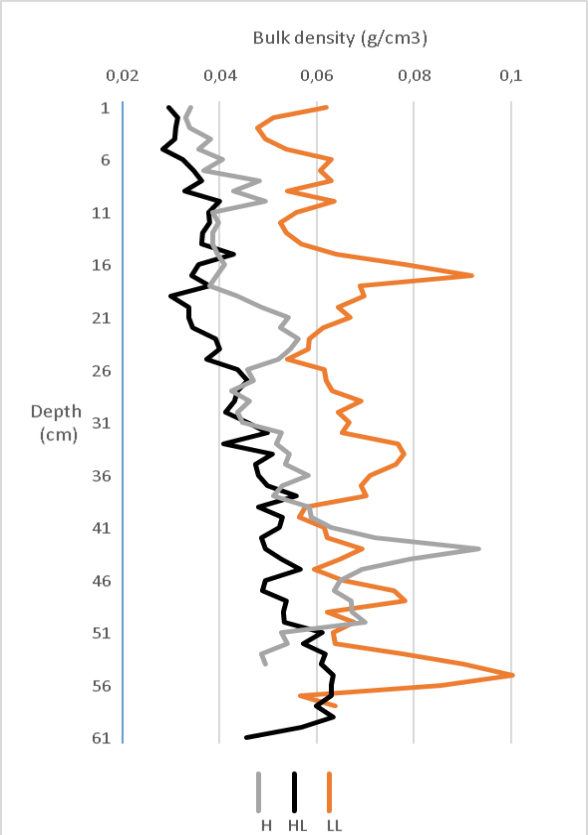


Figure 9. Bulk densities for each of the three cores, H, HL and LL. Lines show the measured values at each depth. Density generally increases in each core towards deeper subsamples.

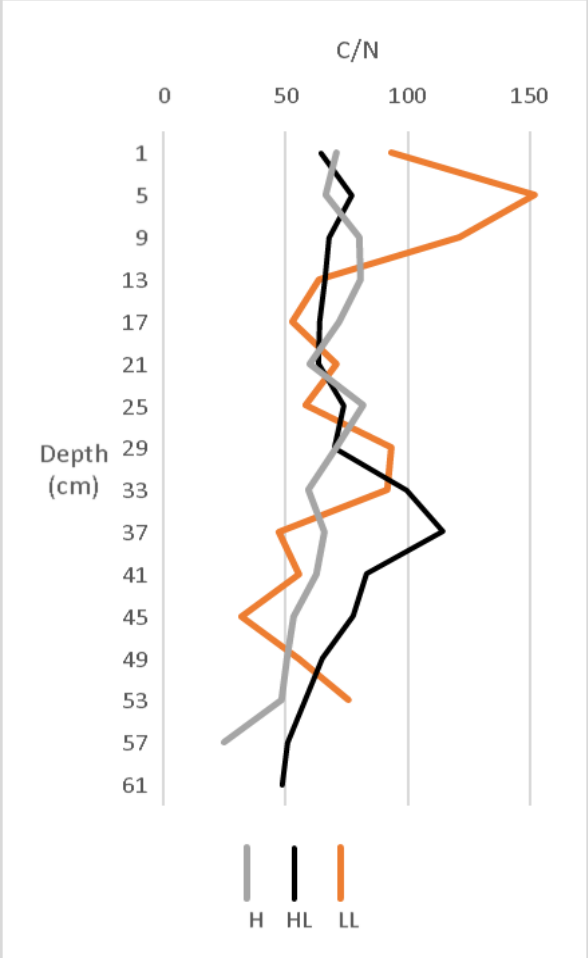


Figure 10. C/N ratios for each of the three cores, H, HL and LL. Lines show the measured values at each depth. C/N ratio drops in each core towards deeper subsamples. Especially HL core has a very steady C/N ratio throughout the core.

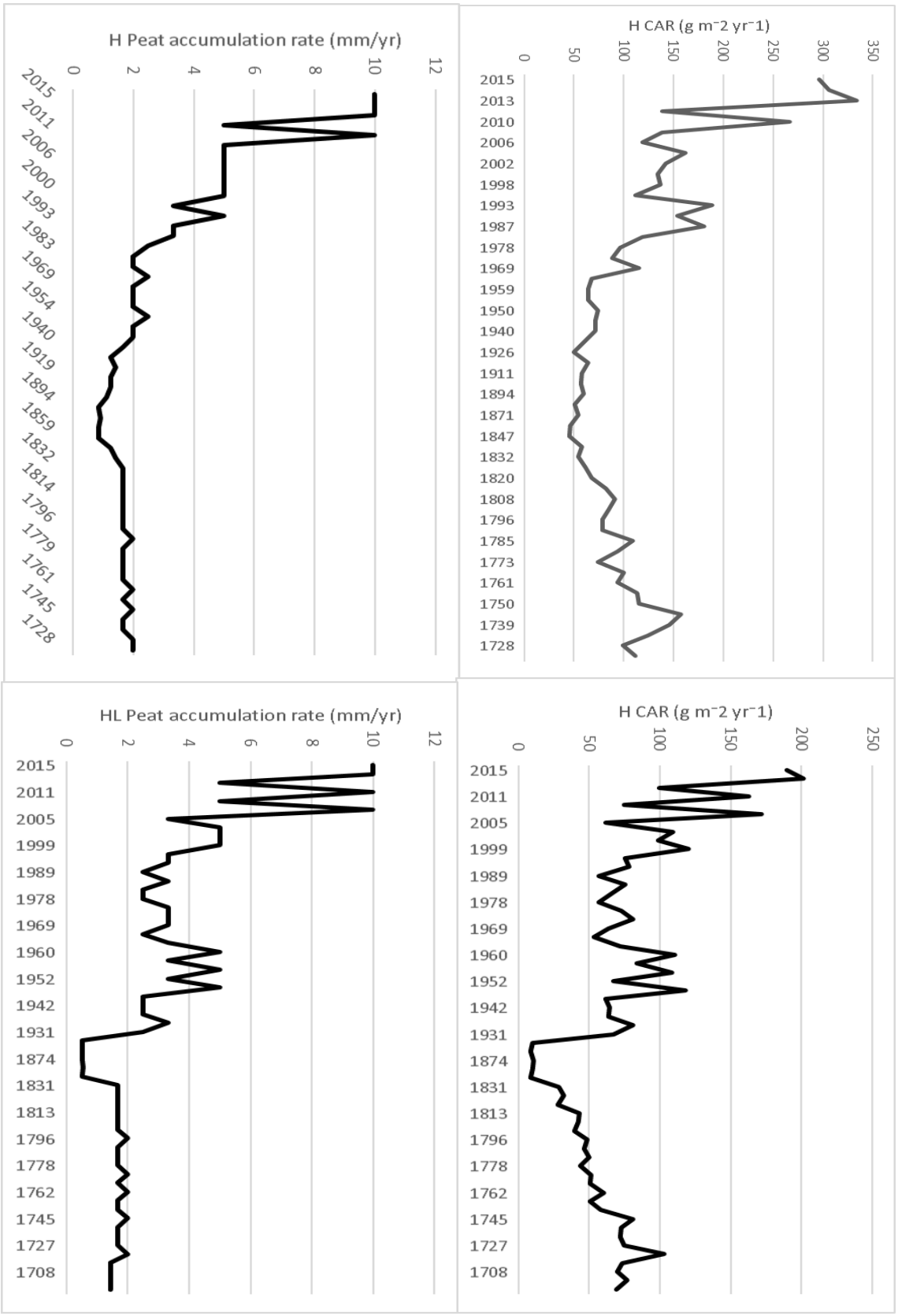
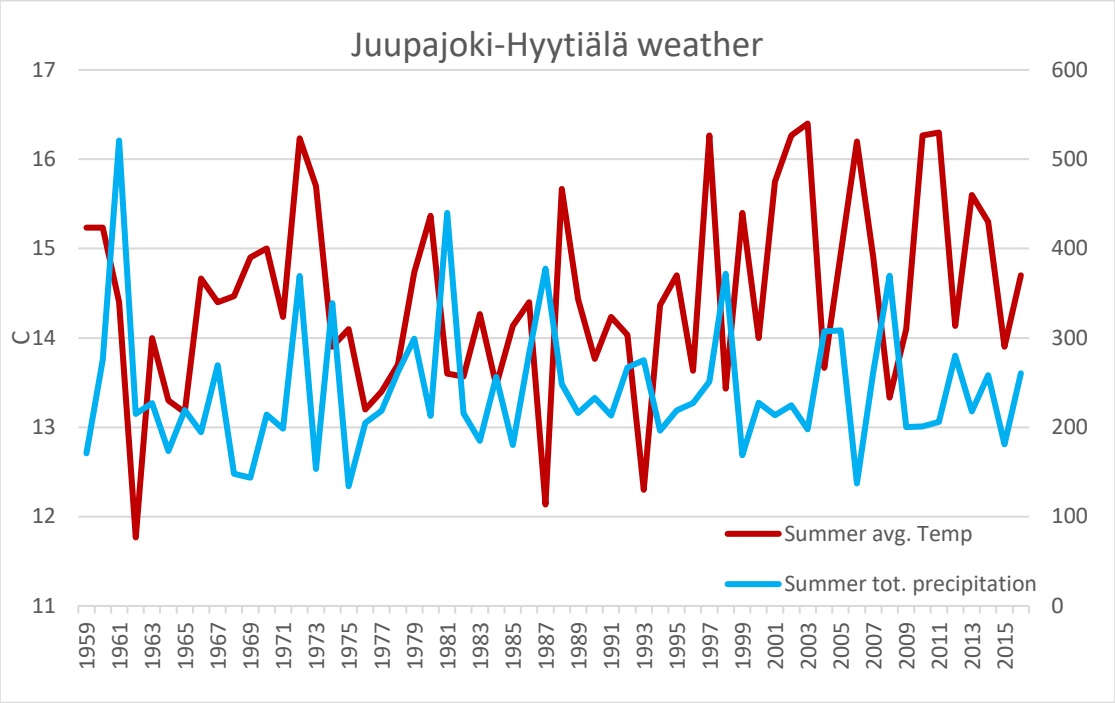


Figure 11. Top: H section peat accumulation rate and apparent C accumulation rate. Bottom: HL section peat accumulation rate and apparent C accumulation rate. Y-axes are Anno Domini years provided by the age-depth models.

4.5. Hyytiälä weather data

From Juupajoki-Hyytiälä weather station temperature and rainfall data is available from 1959. Data is provided for free use by Ilmatieteenlaitos. In figure 12 average summer (June-August) temperature and total summer precipitation are shown. There is no clear pattern in precipitation data, but in temperatures a rise in the late 1990's towards current warmer summers is present, with an identified changepoint at year 1996 AD (Fig. 12).



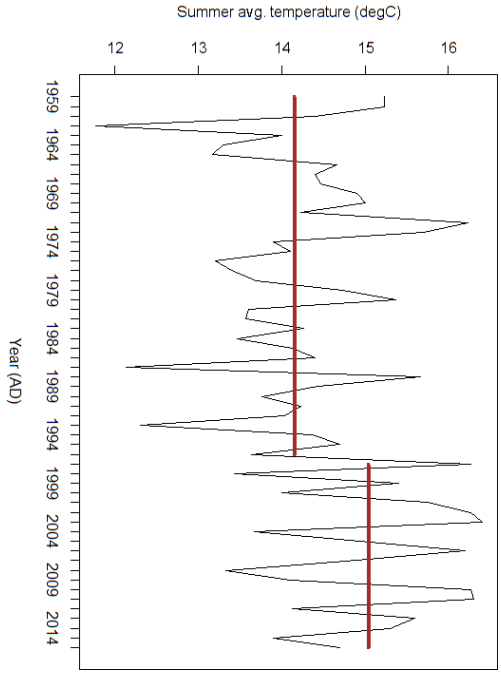


Figure 12. Up: Weather data from Juupajoki-Hyytiälä weather station in the proximity of Lakkasuo. Red line is average summer temperature (°C) and blue line is total summer precipitation (mm).

Left: Changepoint analysis for measured mean summer (June-August) temperatures, changepoint at 1996 AD. Precipitation data did not yield a sensible changepoint outcome.

4.6. Changepoint analysis results for palaeo data

Plant macrofossil data was combined into functional groups “dry”, “intermediate” and “wet” to statistically analyse changes in plant assemblages. As *Sphagnum* was dominating the cores, also these groups were characterized by *Sphagnums*; *S. fuscum* for dry, *S. rubellum, S. balticum* and *S.* sect *Sphagnum* for intermediate and *S.* sect. *cuspidata* for wet habitat. These are similar to plant functional types for hummock, lawn and hollow described by Tuittila *et al.* (2013). Other taxa from plant macrofossil data was also included, but their role was relative diminished as they were outnumbered by *Sphagnum.* Some species were harder to place in a definite group, e.g. *S. rubellum* and *E. vaginatum*, as they have wide WTD tolerance (Rydin and Mcdonald, 1985). These species were placed in the “intermediate” group, as they seemed most likely to occur with other intermediate species.

Results of the changepoint analyses for plant macrofossil data is visualised in figure 13. Multiple changepoints were identified in most of the groups in each habitat. In HL section (Fig. 13A-C) a changepoint c. 1790 AD from wetter habitat towards intermediate taxa is observed. Change follows the depth 46 cm in the macrofossil data, which sees a peak in hollow-tolerant *Sphagnum* sect. *cuspidata.* A changepoint at 1965 AD indicates drying of the HL habitat, which coincides with the appearance of *S. fuscum* in the macrofossil data. A peak in the dry taxa is identified as a changepoint at 2003 AD. Another changepoint was identified in the dry taxa at 2014 AD (Fig. 13A), which was not identified in the intermediate taxa. Only one changepoint was identified in the intermediate taxa in the same time period as dry taxa goes through three prompting questions about the nature of drying in the HL habitat. As analysis was done using “PELT” function to identify multiple changes, it is possible that these drying shifts would be more truthfully expressed as a single changepoint.

In the H section, first a change towards drier habitat is between c. 1756-1779 AD (Fig. 13D-F). Interestingly, after the downfall of wet taxa, first changepoint was identified in the dry taxa, and only a little later in the intermediate taxa. This can also be interpret fom the macrofossil data, as *S. fuscum* rises slightly more prominently than intermediate *S. balticum* falls. Further drying is visible during the 20th century, again first in the dry taxa followed by intermediate taxa with changepoints at 1926 AD and 1969 AD respectively.

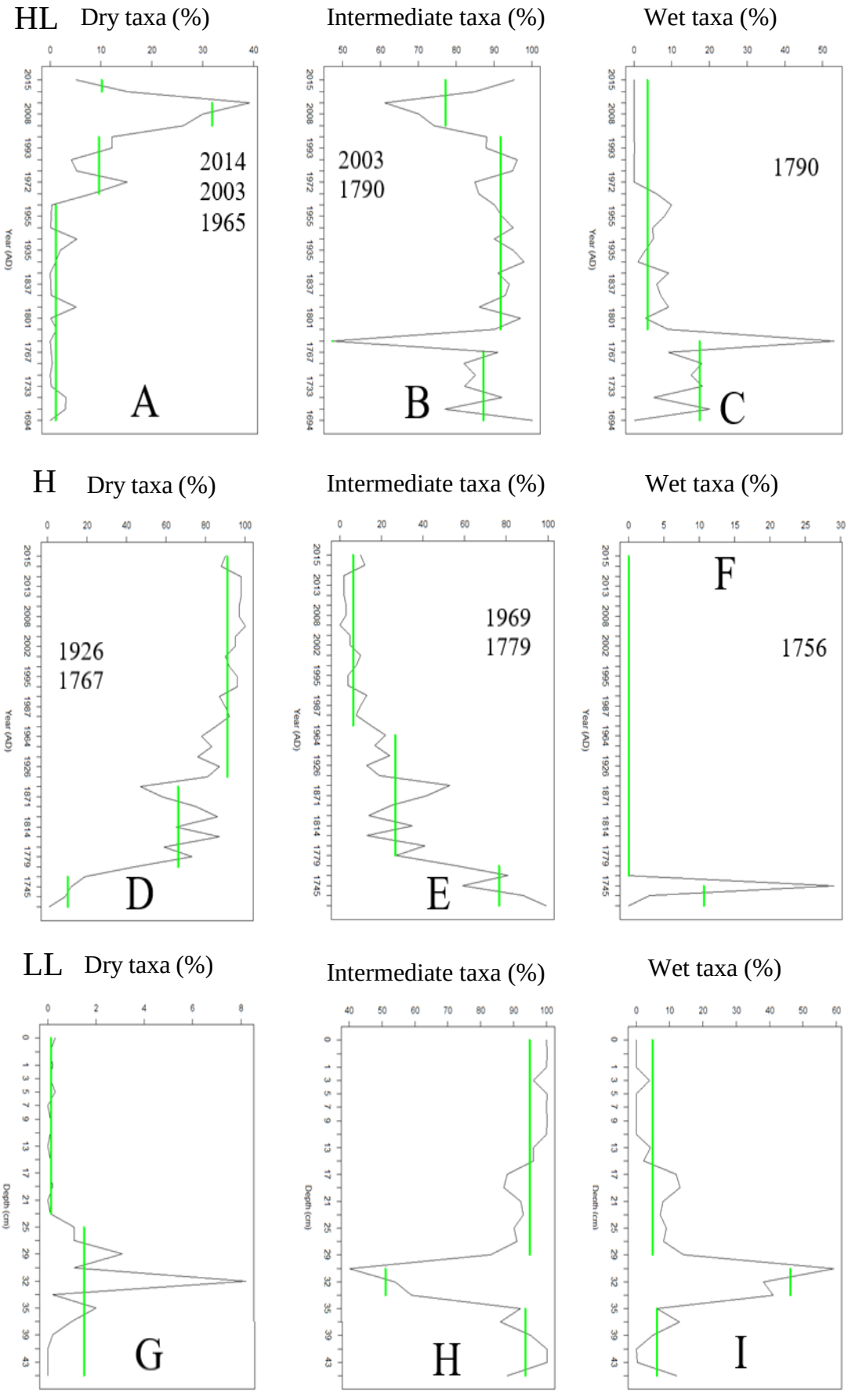

HL
Dry taxa (%)
Intermediate taxa (%)
Wet taxa (%)
2014
2003
1965
2003
1790
1790
A
B
C
H
Dry taxa (%)
Intermediate taxa (%)
Wet taxa (%)
1926
1767
1969
1779
1756
D
E
F
LL
Dry taxa (%)
Intermediate taxa (%)
Wet taxa (%)
G
H
I
Year (AD)
Depth (cm)

Figure 13. Changepoint analyses results for macrofossil data. Each core was analysed for dry, intermediate and wet taxa (%) separately, A-C high lawn, D-F hummock, G-I low lawn. Changepoints are highlighted as green lines. A-F y-axes are Anno Domini years provided by the age-depth models. G-I y-axes are depth (cm). Note different values in x-axes. Inferred years for change points in A-F are based on age-depth models.

The LL section was not dated and the changepoints identified cannot thus be correlated with age (Fig. 13G-I). Changes in the LL macrofossil data is less clear as all detected taxa: *S.* sect. *Sphagnum, S. rubellum* and *S. balticum* fall under the intermediate category. Therefore, the LL section does not experience a change point in the top 20cm, unlike HL and H, as only the relative proportions of intermediate species changed. However, changepoints before and after the wet phase between 34-30 cm were identified. Dry taxa were very sparse, and changepoint at 25 cm is not very informative.

Changepoints for peat properties in H and HL cores are shown in figure 14. As both accumulation curves closely follow each other, a changepoint is expected at the same time in both values. However, in HL (Fig. 14A-B) changepoint for peat accumulation is dated to c. 1837 and for carbon accumulation to c. 1999, compared to H core (Fig. 14C-D), where the changepoints are dated to c. 1987 for both accumulation rates respectively. A rise in accumulation rates following a preceding drop at 1837 is present at both cores and accumulation rates, but interestingly the changepoint analysis is only identifying the change in HL peat accumulation rate. The relatively high carbon accumulation at the bottom of both cores, due to high carbon content of the peat, was not recorded in the changepoint analysis, as only one changepoint was identified.

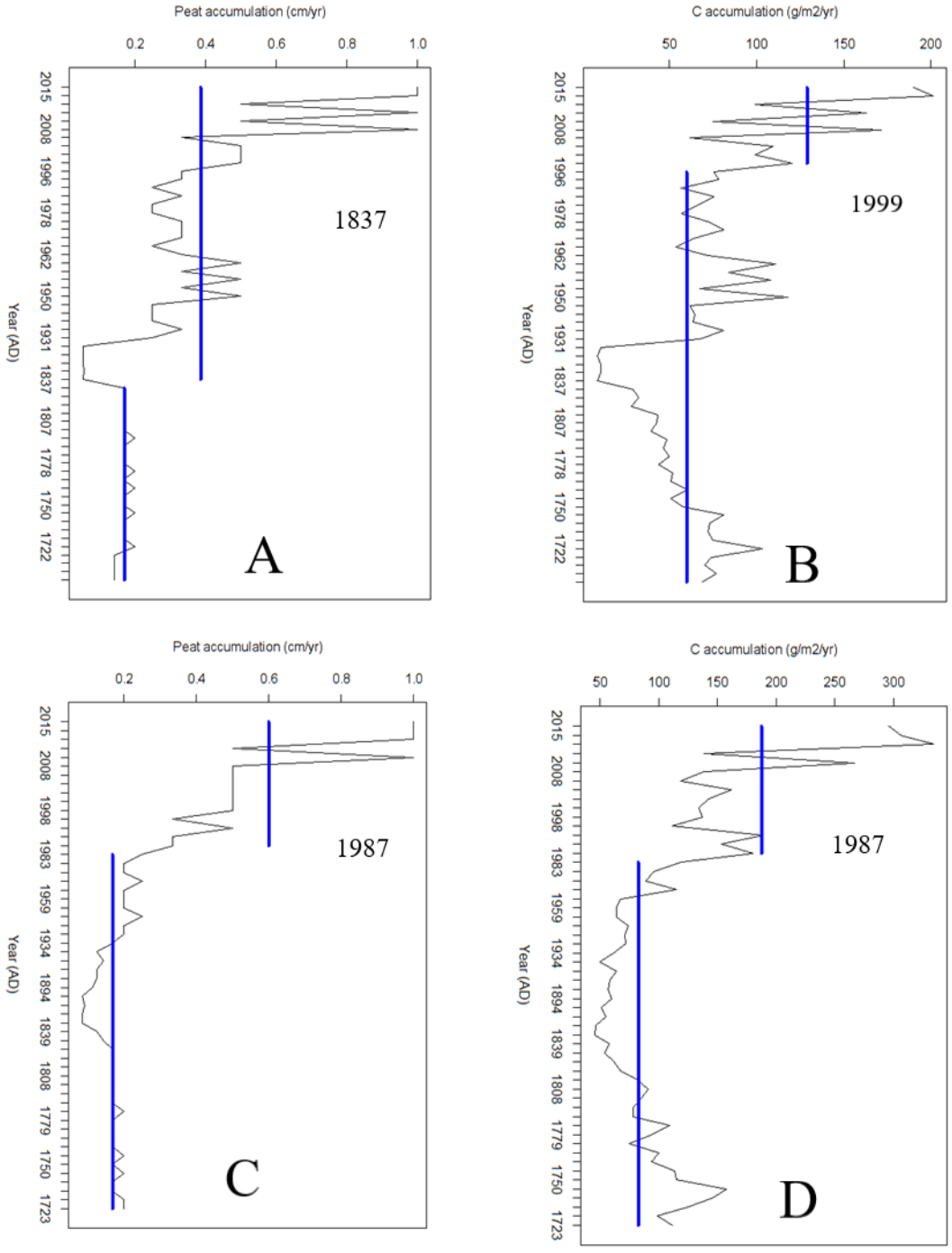


Figure 14. Changepoints for peat and carbon accumulation rates for HL (A and B) and H (C and D). Y-axes are Anno Domini years provided by the age-depth models. Approximate years of the changepoints in A-D are from age-depth models.

5. DISCUSSION

5.1. Vegetation changes and link to climate

The results of macrofossil data and changepoint analysis reveal the development of the sample sites to their current vegetation composition and microform. Climate is the probable cause for changes in plant assemblages in macrofossil data. LIA is associated with wetter habitats, which has also been found in Lakkasuo palaeodata (Tuittila et al., 2007; Väliranta et al., 2007). Post-LIA warming dates simultaneous to the drying in Lakkasuo. Vegetation history tells about the moisture conditions, and when dated it can be used to link changes to climatic variations. Climate-induced changes in vegetation lead to long-term shifts in peatland carbon balance in addition to direct changes (Bardgett et al., 2013).

All microforms that were analysed here, hummock, high and low lawn, show some changes in their vegetation compositions through time indicating changes in water regime and therefore microform. These habitats were chosen exactly for the reason that their vegetation is prone to shifts, even if the vegetation in bog remains generally similar for centuries or millennia (Baird et al., 2016; Kokkonen et al., 2019). Most prominent changes are in the H microform, which shows a gradual drying with two changepoints identified c. 1750-1780 AD and in the 20th century. The vegetation composition before the first changepoint is very similar to current HL vegetation, proving that microform in the sample location has changed indeed from high lawn closer to WTD characteristic for hummocks.

HL has also dried, but mostly same taxa, namely *S. balticum,* have been present for most of the investigated time period. A change of microform is not as clear as in H, but during the wetter stages in the 18th century vegetation seems to resemble more low lawn habitat or even hollow with distinctive amounts of *S.* sect. *cuspidata.* A wet period is observed in the 18th century and dry period during 2000's. The wet periods are dated to the LIA, when climate was colder. The dry phase, especially the latest part can be in turn linked to recent warming starting in 1980's and exemplified in the 21st century. Interestingly, an increase in moisture few years before the year 2016 based on local meteorological data (Fig. 12) is visible in both H and HL. This lends to support to the hypothesis that these microforms are sensitive to moisture changes and are thus suitable for climate

reconstructions. Generally, HL results are congruent with testate amoeba analysis and WTD reconstruction done from the same section (Fig. 15).

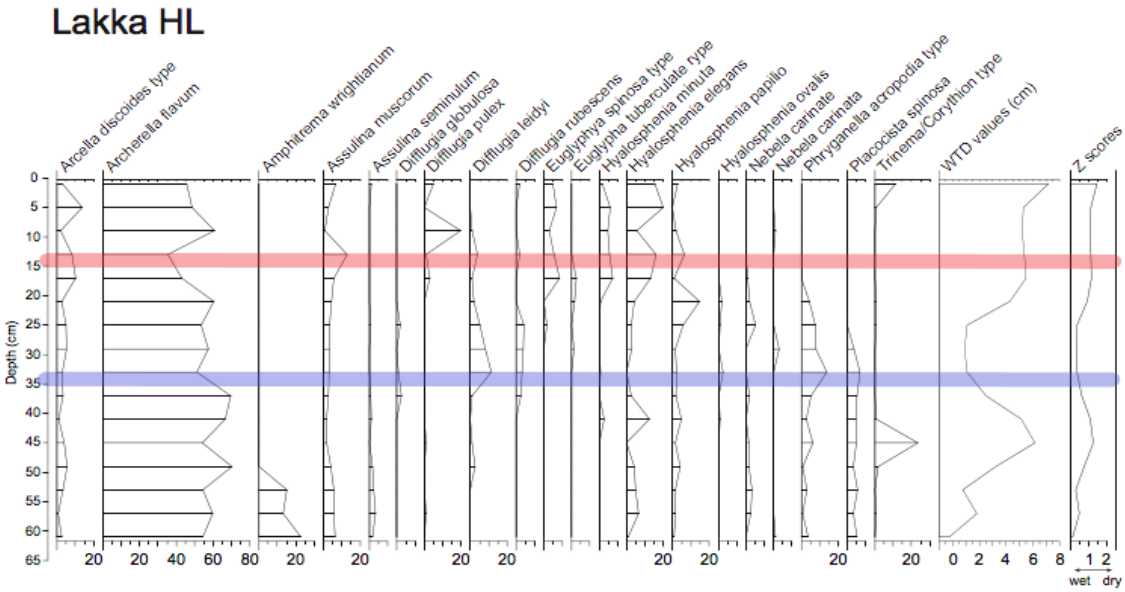


Figure 15. Testate amoeba analysis and interpreted WTD values for HL core. Analysis was done by the research team member Hui Zhang. The offset of LIA is marked with a blue line and the onset of current warming with a red line.

In the wettest LL core vegetation goes through one major shift as *S.* sect. *sphagnum* and *S. balticum* are replaced by *S. rubellum*. This shift is marked with an extremely wet short period with an abrupt rise of *S.* sect. *cuspidata* interrupting the increase of *S. rubellum*. During this wet event vegetation composition resembled hollow conditions, while before and after low lawn habitat exists. The conditions at the bottom of the core are slightly more wet than in the top part. Because the LL core was not dated throughout, the age of this shift in vegetation remains unknown. However, tentatively based on depth it is at the same time as the similar shift in the adjacent HL core, thus happening around the end of LIA. Similar wet phases before drying towards modern times were observed in all cores.

All the cores were dominated by *Sphagna* but the proportional shares of different taxa varied in peat cores. Some short-lasting events of dry *Sphagnum* species living under wet conditions, or vice-versa, are possible (Rydin and Mcdonald, 1985; Väliranta et al., 2012), and such events have taken place also in Lakkasuo. Additional short-lived extremely wet periods characterised by *S.* sect. *cuspidata* are found in HL an LL. Generally in the macrofossil data, plant assemblages of dominating *Sphagna* often remain constant until a

strong-enough forcing creates a shift. It is reasonable to expect based on macrofossil data that in Lakkasuo during the last c. 300 years, *Sphagnum* has been the controlling vegetation element, whose abundancies and species compositions are following environmental variability, while the other bog vegetation adapts to *Sphagnum* dominance. The macrofossil data show that a shift from microform is not instantaneous, but a dynamic process. Changepoints were used to pinpoint the possible 'point of no return', when another type of habitat conditions take over.

A general drying is visible in data as suggested by plant macrofossil analysis and changepoint analysis. Similar to results from same site (Zhang et al., 2020) and from another site from southern Finland (Väliranta et al., 2007), WTD drawdown and drying started c. 1800 AD and plant assemblages have adapted. In HL and H cores a change from hollow/lawn species, e.g. *S. cuspidatum/S. balticum*, to hummock species was more abrupt than in LL, where change is more gradual, and hummock species have not appeared at all. In LL plant macrofossil data drying is indicated by *S. rubellum,* and it isn't visible in the changepoint analysis, as this widely tolerant species was interpreted to represent lawn habitat rather than drier hummock, where to some extent *S. rubellum* can also thrive (Väliranta et al., 2007). My data also supports the role of *S. fuscum* as indicator of drying, as drying changepoints are marked following rise in *S. fuscum* proportions. It is also noteworthy that *E. vaginatum* can signal the change towards hummock type vegetation (Mathijssen et al., 2016), as in H at the end of LIA, even though it is most abundant at intermediate WTD (Väliranta et al., 2007; Tuittila et al., 2013).

An annual scale comparison between Hyytiälä weather data and macrofossil data point to the role of warm summers acting as a starting point for microform drying (Charman, 2007). This is potentially observed in HL core in the late 1960's and early 1970's as consequent warm summers are concurrent with the rise of *S. fuscum*. The current warming is also accompanied by the rise of dry taxa. Precipitation's effect on peatland vegetation dynamics is harder to predict, but some drying could be linked to summers of low precipitation. The effects of increased temperature outweigh the possible increased moisture in peatlands caused by wet summers. Overall, the rise in summer temperatures with steady precipitation levels has led to a change in effective moisture towards dryer conditions.

Widespread drying of northern peatlands has been recorded during the last centuries (Swindles et al., 2019), and Lakkasuo data seem to correspond this. Hydrological conditions in peatlands control the carbon dynamics, which makes drying development crucial to understand. Eventually drying leads to increase in decomposition resulting in a release of carbon back into atmosphere (Gill et al., 2017; Swindles et al., 2019). In Lakkasuo current drying has been recorded with accompanying increase in hummock-type vegetation (Kokkonen et al., 2019) and further drying may lead to a shift from one functional plant type to another; for example from *Sphagnum* to drier shrub habitat, which would have a drastic impact on the peatland carbon dynamics increasing both the CO_2 uptake in peat oxidation (Munir et al., 2014). Even though in the plant macrofossil record the plant functional type *per se*, i.e. *Sphagnum*-dominance, has not changed, the recorded drying may enable establishment of for drier taxa to Lakkasuo.

5.2. Peat properties and carbon accumulation

Bulk density and C/N ratios of HL and H are typical for *Sphagnum* peat (Chambers et al., 2010; Loisel et al., 2014). Bulk density values varied between 0,02836 g/ cm^3 and 0,10026 g/ cm^3 with HL having lowest average and H the highest. C/N ratios were between values 152 and 25. HL values were slightly higher than H and LL values. Both density and C/N are associated to depth and thus also age. Bulk density tends to increase with depth as peat is compressed, while C/N values decrease due to decay (Malmer and Wallén, 2004; Loisel et al., 2014). Peat accumulation rates for both cores are low at 0.2 cm yr^{-1} before the end of LIA, i.e. around the beginning of the 20^{th} century. After this HL peat accumulation rates rise probably because of warmer temperatures accounting for increased productivity. In the H core peat accumulation rates do not rise significantly before c. 1987 AD, when current warming starts. In HL this rise also occurs and mean peat accumulation rate for both cores between 1986 and 2016 is around 0.5 cm yr^{-1}.

Carbon accumulation in HL and H was relatively high at the bottom of the cores c. 1700-1800 AD, with values between 50 and 150 g(C) m^{-2} yr^{-1}. A steady decline culminates at the terminal stages of LIA, c. 1870-1910, after which a sharp rise is recorded. Overall, carbon and peat accumulation rates turn to a sharp rise at the offset of LIA. The accumulation is accelerated even more c. 1980-1990's together with increased temperatures as also pointed out by changepoint analysis. Carbon accumulation reaches very high peaks at both cores for the topmost subsamples. Carbon accumulation in

peatlands is strongly controlled by local climate (e.g. Malmer and Wallén, 2004; Frolking et al., 2010) and surface vegetation (Loisel and Yu, 2013b). Warming is related benefits carbon uptake while dry *S. fuscum* dominated habitats are effective at sequestrating carbon (Clymo et al., 1998; Loisel et al., 2012; Loisel and Yu, 2013a; Charman et al., 2013; Gallego-Sala et al., 2018). Due to these factors current (2000-2016) average carbon accumulation rates in Lakkasuo are nearly double as high as before. Noteworthy is that the whole peat section is young poorly decomposed also at the bottommost section (Fig. 2).

The impact of future warming for peatland carbon balance is not entirely resolved, because warmer temperatures increase microbial decomposition of peat and drying of peat surface releasing carbon (Dorrepaal et al., 2009; Swindles et al., 2019). Based on palaeoecological data, it is predicted that the rise of NPP and carbon uptake of peatlands will be greater than the loss because of increased decomposition (e.g. Charman et al., 2013; Loisel and Yu, 2013a; Gallego-Sala et al., 2018). Since Lakkasuo has accumulated a large amount of carbon recently, a change to a carbon source by aforementioned factors could potentially release carbon back to atmosphere with an unknown pace. Decrease in the carbon accumulation has been predicted in Lakkasuo (Kokkonen et al., 2019). Carbon accumulation is controlled by vegetation, hydrology and temperature and changes are reflected in microtopography dynamics, especially lawns are sensitive habitats. Because vegetation shifts affect the carbon balance of peatland, understanding vegetation-climate interactions are vital (Loisel and Yu, 2013b).

5.3. Potential sources of error

When analysing peat macrofossils, one should always note that some species are much more resistant towards decay in the peat profile. This means that for example *Sphagnum* remains and hard tissue such as roots better preserved than other taxa and softer tissue. Role of degradation should therefore be kept in mind when interpreting the results. Mostly the Lakkasuo cores were poorly decomposed, i.e. intact, and material for macrofossil analysis was easy to identify, but at some points more decomposed material made it challenging to count the proportions. This was evident at the bottom of the cores, where material was distinctly differing from the rest of the cores. Furthermore, as the macrofossil analysis is done from a small subsample, small occurrences of plants in each sample may be randomly mssing or captured during the analysis.

Errors occurring during the dating process are possible although careful measures were taken to avoid them and the possibility of contamination for radiocarbon dating was taken extremely seriously as it is susceptible to contamination by modern carbon. Sample preparation for dating included many steps where samples were handled and moved around. For lead 210 -method, laboratory process included many steps, and one sample was lost during the process, while another was supposedly spiked twice with Polonium. For unknown reason for this study the Radiocarbon results did not seem to yield accurate results, and for H and HL dates do not perfectly coincide with the ^{210}Pb age, which are considered more reliable for young sediments.

The age models are used to connect data to a time period, but as models they are only projections of possibilities instead of actual time values. Mathematical errors always exist, even when statistical analyses are carefully carried out. Pioneering application of Changepoint analysis proceed via trial and error in this study. Although some previous palaeo applications exist, as a novel approach, the application could be further developed.

6. CONCLUSIONS

Centennial to decadal changes in Lakkasuo macrofossil record seem to be related to climate changes and weather conditions. The bog plant species compositions reacted to known climatic trends, i.e. LIA and recent warming, and local precipitation and temperature patterns. Trends observed in carefully dated data, in centennial-decadal scale, can be used to understand and predict future bog dynamics, including drying. My data suggest that warming will alter peatland vegetation via drying and thus carbon dynamics will change.

I used high-resolution plant macrofossil data and chronological data investigate changes in vegetation composition and interpret moisture conditions in Lakkasuo over the past c. 300 years. Peat property analyses and carbon accumulation rate calculations provided supporting data of the dynamics of a studied boreal bog. I included changepoint analysis to enhance the signal recorded in palaeo-data. Changepoint is a useful tool to pinpoint exactly the changes, for example to identify vegetation shifts due to changing climate as was done here. Further, it correlates multiple datasets with each other to depict, if changes occurred simultaneously suggesting a common driving force. Although changepoint is a relatively novel method bog vegetation history studies, the method has yielded promising

results in Antarctic moss bank studies (Amesbury et al., 2017). Changepoint analysis has potential to help in identifying the important past shifts occur in vegetation and hence associated carbon dynamics. I conclude that this method could be developed further to address better this kind of research questions and datasets.

Overall, the studied bog vegetation communities in Lakkasuo have experienced some variation over the past centuries as a response to changes in climate. I investigated small scale-variations in peatland vegetation to understand relation between vegetation, climate and carbon dynamics. The records reveal a drying in all studied three microhabitats. Associated with increase in peat and carbon accumulation these changes were linked to major climatic periods and local weather data. Correlation between warming and shift towards drier bog taxa was evident with simultaneous increase in carbon accumulation rates.

I conclude that my findings generally support the current understanding of peatland-climate interactions. This work brought forth insight about vegetation patterns inside a bog within centuries and decades to better understand past and future changes. However, to make a more robust interpretations that these shifts were exclusively caused by climate, more data are needed. Similarly, even stronger and longer chronologies would help making solid conclusions.

7. ACKNOWLEDGEMENTS

I want to thank Minna Väliranta for excellent supervision and patience. I also express my gratitude towards Eeva-Stiina Tuittila and Hui Zhang. Thank you Sanna Piilo for help with everything and all the fun moments. Most of all I want to thank Mimi for making me do this.

REFERENCES

Alm, J., Schulman, L., Walden, J., Nykanen, H., Martikainen, P.J., Silvola', J., 1999. Carbon Balance of a Boreal Bog during a Year with an Exceptionally Dry Summer. Ecology 80, 161–174.

Amesbury, M.J., Roland, T.P., Royles, J., Hodgson, D.A., Convey, P., Griffiths, H., Charman, D.J., 2017. Widespread Biological Response to Rapid Warming on the Antarctic Peninsula. Current Biology 27, 1616-1622.e2. https://doi.org/10.1016/j.cub.2017.04.034

Anchukaitis, K.J., Wilson, R., Briffa, K.R., Büntgen, U., Cook, E.R., D'Arrigo, R., Davi, N., Esper, J., Frank, D., Gunnarson, B.E., Hegerl, G., Helama, S., Klesse, S., Krusic, P.J., Linderholm, H.W., Myglan, V., Osborn, T.J., Zhang, P., Rydval, M., Schneider, L., Schurer, A., Wiles, G., Zorita, E., 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163, 1–22. https://doi.org/10.1016/j.quascirev.2017.02.020

Baird, A.J., Milner, A.M., Blundell, A., Swindles, G.T., Morris, P.J., 2016. Microform-scale variations in peatland permeability and their ecohydrological implications. Journal of Ecology 104, 531–544. https://doi.org/10.1111/1365-2745.12530

Bardgett, R.D., Manning, P., Morriën, E., De Vries, F.T., 2013. Hierarchical responses of plant-soil interactions to climate change: consequences for the global carbon cycle. J Ecol 101, 334–343. https://doi.org/10.1111/1365-2745.12043

Blunier, T., Chappellaz, J., Schwander, J., Stauffer, B., Raynaud, D., 1995. Variations in atmospheric methane concentration during the Holocene epoch. Nature 374, 46–49. https://doi.org/10.1038/374046a0

Bradley, R.S., 2014. Paleoclimatology: Reconstructing Climates of the Quaternary. Elsevier Science & Technology, Saint Louis, UNITED STATES.

Chambers, F., Beilman, D., Yu, Z., 2010. Methods for determining peat humification and for quantifying peat bulk density, organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. Mires and Peat 7, 1–10.

Charman, D., 2002. Peatlands and environmental change. John Wiley & Sons.

Charman, D.J., 2007. Summer water deficit variability controls on peatland water-table changes: implications for Holocene palaeoclimate reconstructions. The Holocene 17, 217–227. https://doi.org/10.1177/0959683607075836

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., der Linden, M. van, De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Roux, G.L., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D.H., Zhao, Y., 2013. Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences; Katlenburg-Lindau 10, 929. http://dx.doi.org.libproxy.helsinki.fi/10.5194/bg-10-929-2013

Clymo, R.S., 1984. The limits to peat bog growth. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 303, 605–654. https://doi.org/10.1098/rstb.1984.0002

Clymo, R.S., Hayward, P.M., 1982. Biology of Sphagnum, in: Bryophyte Ecology, Edited by A. J. E. Smith. CRC Press,Boca Raton, Fla., pp. 229–289.

Clymo, R.S., Turunen, J., Tolonen, K., 1998. Carbon Accumulation in Peatland. Oikos 81, 368–388. https://doi.org/10.2307/3547057

Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1. https://doi.org/10.1126/sciadv.1400082

Crowley, T.J., 2000. Causes of climate change over the past 1000 years. Science 289, 270–277. https://doi.org/10.1126/science.289.5477.270

Diaz, H.F., Trigo, R., Hughes, M.K., Mann, M.E., Xoplaki, E., Barriopedro, D., 2011. Spatial and Temporal Characteristics of Climate in Medieval Times Revisited. Bull. Amer. Meteor. Soc. 92, 1487–1500. https://doi.org/10.1175/BAMS-D-10-05003.1

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., Aerts, R., 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619. https://doi.org/10.1038/nature08216

Fairbanks, R.G., 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature 342, 637–642. https://doi.org/10.1038/342637a0

Finnish Meterological Institute, 2020. Open data - Finnish Meteorological Institute. Retrieved from https://www.ilmatieteenlaitos.fi/havaintojen-lataus#!/.

Frolking, S., Roulet, N.T., 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Global Change Biology 13, 1079–1088. https://doi.org/10.1111/j.1365-2486.2007.01339.x

Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J., Richard, P.J.H., 2010. A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. Earth Syst. Dynam. 1, 1–21. https://doi.org/10.5194/esd-1-1-2010

Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T., Bochicchio, C., Booth, R.K., Bunbury, J., Camill, P., Carless, D., Chimner, R.A., Clifford, M., Cressey, E., Courtney-Mustaphi, C., De Vleeschouwer, F., de Jong, R., Fialkiewicz-Koziel, B., Finkelstein, S.A., Garneau, M., Githumbi, E., Hribjlan, J., Holmquist, J., Hughes, P.D.M., Jones, C., Jones, M.C., Karofeld, E., Klein, E.S., Kokfelt, U., Korhola, A., Lacourse, T., Le Roux, G., Lamentowicz, M., Large, D., Lavoie, M., Loisel, J., Mackay, H., MacDonald, G.M., Makila, M., Magnan, G., Marchant, R., Marcisz, K., Martínez Cortizas, A., Massa, C., Mathijssen, P., Mauquoy, D., Mighall, T., Mitchell, F.J.G., Moss, P., Nichols, J., Oksanen, P.O., Orme, L., Packalen, M.S., Robinson, S., Roland, T.P., Sanderson, N.K., Sannel, A.B.K., Silva-Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J., Väliranta, M., van Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells, J., Zhao, Y., 2018. Latitudinal limits to the predicted increase of the peatland carbon sink with warming. Nature Clim Change 8, 907–913. https://doi.org/10.1038/s41558-018-0271-1

Gill, A.L., Giasson, M.-A., Yu, R., Finzi, A.C., 2017. Deep peat warming increases surface methane and carbon dioxide emissions in a black spruce-dominated ombrotrophic bog. Global Change Biology 23, 5398–5411. https://doi.org/10.1111/gcb.13806

Goosse, H., Renssen, H., Timmermann, A., Bradley, R.S., Mann, M.E., 2006. Using paleoclimate proxy-data to select optimal realisations in an ensemble of simulations of the climate of the past millennium. Clim Dyn 27, 165–184. https://doi.org/10.1007/s00382-006-0128-6

Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecological Applications 1, 182–195. https://doi.org/10.2307/1941811

Granath, G., Strengbom, J., Rydin, H., 2010. Rapid ecosystem shifts in peatlands: linking plant physiology and succession. Ecology 91, 3047–3056.

Gunnarsson, U., 2005. Global patterns of Sphagnum productivity. Journal of Bryology 27, 269–279. https://doi.org/10.1179/174328205X70029

Ingram, H. a. P., 1978. Soil Layers in Mires: Function and Terminology. Journal of Soil Science 29, 224–227. https://doi.org/10.1111/j.1365-2389.1978.tb02053.x

IPCC, 2013a. Annex I: Atlas of global and regional climate projections., in: Stoker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovern-Mental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535.

IPCC, 2013b. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Juottonen, H., Kotiaho, M., Robinson, D., Merilä, P., Fritze, H., Tuittila, E.-S., 2015. Microform-related community patterns of methane-cycling microbes in boreal *Sphagnum* bogs are site specific. FEMS Microbiology Ecology 91, fiv094. https://doi.org/10.1093/femsec/fiv094

Killick, R., 2014. Changepoint: An R Package for Changepoint Analysis. Journal of Statistical Software 58, 1.

Kokkonen, N.A.K., Laine, A.M., Laine, J., Vasander, H., Kurki, K., Gong, J., Tuittila, E.-S., 2019. Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. Journal of Vegetation Science 30, 1206–1216. https://doi.org/10.1111/jvs.12794

Korhola, A., 1996. Initiation of a sloping mire complex in southwestern Finland: Autogenic *versus* allogenic controls. Écoscience 3, 216–222. https://doi.org/10.1080/11956860.1996.11682334

Korhola, A., 1992. Mire induction, ecosystem dynamics and lateral extension on raised bogs in the southern coastal area of Finland. Fennia - International Journal of Geography 170, 25–94.

Korhola, A., Ruppel, M., Seppä, H., Väliranta, M., Virtanen, T., Weckström, J., 2010. The importance of northern peatland expansion to the late-Holocene rise of atmospheric methane. Quaternary Science Reviews 29, 611–617. https://doi.org/10.1016/j.quascirev.2009.12.010

Kuhry, P., 1994. The Role of Fire in the Development of Sphagnum-Dominated Peatlands in Western Boreal Canada. Journal of Ecology 82, 899–910. https://doi.org/10.2307/2261453

Laine, A., Riutta, T., Juutinen, S., Väliranta, M., Tuittila, E.-S., 2009. Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. Ecological Modelling 220, 2646–2655. https://doi.org/10.1016/j.ecolmodel.2009.06.047

Laine, J., Komulainen, V.-M., Laiho, R., Minkkinen, K., Rasinmäki, A., Sallantaus, T., Sarkkola, S., Silvan, N., Tolonen, K., Tuittila, E.-S., Vasander, H., Päivänen, J., 2004. Lakkasuo: a guide to mire ecosystem, Helsingin yliopiston Metsäekologian laitoksen julkaisuja. Univ. of Helsinki, Dep. of Forest Ecology, Helsinki.

Laine, J., Minkkinen, K., Laiho, R., Tuittila, E.-S., Vasander, H., 2000. Suokasvit, turpeen tekijät = Mire vegetation and peat formation, Helsingin yliopiston metsäekologian laitoksen julkaisuja. University of Helsinki, Depart. of Forest Ecology, Helsinki.

Linderholm, H.W., Nicolle, M., Francus, P., Gajewski, K., Helama, S., Korhola, A., Solomina, O., Yu, Z., Zhang, P., D'Andrea, W.J., Debret, M., Divine, D.V., Gunnarson, B.E., Loader, N.J., Massei, N., Seftigen, K., Thomas, E.K., Werner, J., Andersson, S., Berntsson, A., Luoto, T.P., Nevalainen, L., Saarni, S., Väliranta, M., 2018. Arctic hydroclimate variability during the last 2000 years: current understanding and research challenges. Climate of the Past; Katlenburg-Lindau 14, 473–514. http://dx.doi.org.libproxy.helsinki.fi/10.5194/cp-14-473-2018

Loisel, J., Gallego-Sala, A.V., Yu, Z., 2012. Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. Biogeosciences; Katlenburg-Lindau 9, 2737.

Loisel, J., Yu, Z., 2013a. Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. Journal of Geophysical Research: Biogeosciences 118, 41–53. https://doi.org/10.1029/2012JG001978

Loisel, J., Yu, Z., 2013b. Surface vegetation patterning controls carbon accumulation in peatlands. Geophysical Research Letters 40, 5508–5513. https://doi.org/10.1002/grl.50744

Loisel, J., Yu, Z., Beilman, D.W., Camill, P., Alm, J., Amesbury, M.J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L.R., Bunbury, J., Chambers, F.M., Charman, D.J., De Vleeschouwer, F., Fiakiewicz-Kozie, B., Finkelstein, S.A., Gaka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M.C., Klein, E.S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., MacDonald, G., Magnan, G., Mäkilä, M., Mallon, G., Mathijssen, P., Mauquoy, D., McCarroll, J., Moore, T.R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P.J., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A.B.K., Tarnocai, C., Thom, T., Tuittila, E.-S., Turetsky, M., Väliranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y., Zhou, W., 2014. A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. The Holocene; London 24, 1028–1042. http://dx.doi.org.libproxy.helsinki.fi/10.1177/0959683614538073

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., Velichko, A.A., 2006. Rapid Early Development of Circumarctic Peatlands and Atmospheric CH4 and CO2 Variations. Science 314, 285–288. https://doi.org/10.1126/science.1131722

Mäkilä, M., 1997. Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland. Boreas 26, 1–14.

Mäkilä, M., Goslar, T., 2008. The carbon dynamics of surface peat layers in southern and central boreal mires of Finland and Russian Karelia. Suo 59, 49–69.

Mäkilä, M., Moisanen, M., 2007. Holocene lateral expansion and carbon accumulation of Luovuoma, a northern fen in Finnish Lapland. Boreas 36, 198–210.

Malmer, N., Wallén, B., 2004. Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. The Holocene 14, 111–117. https://doi.org/10.1191/0959683604hl693rp

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G., Ni, F., 2009. Global Signatures and Dynamical Origins of the Little Ice Age and Medieval Climate Anomaly. Science 326, 1256–1260. https://doi.org/10.1126/science.1177303

Mathijssen, P.J.H., Kähkölä, N., Tuovinen, J.-P., Lohila, A., Minkkinen, K., Laurila, T., Väliranta, M., 2017. Lateral expansion and carbon exchange of a boreal peatland in Finland resulting in 7000 years of positive radiative forcing. Journal of Geophysical Research: Biogeosciences 122, 562–577. https://doi.org/10.1002/2016JG003749

Mathijssen, P.J.H., Väliranta, M., Korrensalo, A., Alekseychik, P., Vesala, T., Rinne, J., Tuittila, E.-S., 2016. Reconstruction of Holocene carbon dynamics in a large boreal peatland complex, southern Finland. Quaternary Science Reviews 142, 1–15. https://doi.org/10.1016/j.quascirev.2016.04.013

Mauquoy, D., van Geel, B., 2007. Mire and Peat Macros. Elsevier, pp. 2315–2336. https://doi.org/10.1016/B0-444-52747-8/00229-5

McMullen, J.A., Barber, K.E., Johnson, B., 2004. A Paleoecological Perspective of Vegetation Succession on Raised Bog Microforms. Ecological Monographs 74, 45–77. https://doi.org/10.1890/02-4046

Merilä, P., Galand, P.E., Fritze, H., Tuittila, E.-S., Kukko-oja, K., Laine, J., Yrjala, K., 2006. Methanogen Communities Along a Primary Succession Transect of Mire Ecosystems. FEMS Microbiology Ecology 55, 221.

Mikkonen, S., Laine, M., Mäkelä, H.M., Gregow, H., Tuomenvirta, H., Lahtinen, M., Laaksonen, A., 2015. Trends in the average temperature in Finland, 1847–2013. Stoch Environ Res Risk Assess 29, 1521–1529. https://doi.org/10.1007/s00477-014-0992-2

Minkkinen, K., Vasander, H., Jauhiainen, S., Karsisto, M., Laine, J., 1999. Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire, Central Finland. Plant and Soil 207, 107–120. https://doi.org/10.1023/A:1004466330076

Morris, J.L., Väliranta, M., Sillasoo, Ü., Tuittila, E.-S., Korhola, A., 2015. Re-evaluation of late Holocene fire histories of three boreal bogs suggest a link between bog fire and climate. Boreas 44, 60–67. https://doi.org/10.1111/bor.12086

Munir, T.M., Xu, B., Perkins, M., Strack, M., 2014. Responses of carbon dioxide flux and plant biomass to water table drawdown in a treed peatland in northern Alberta: a climate change perspective. Biogeosciences 11, 807–820. https://doi.org/10.5194/bg-11-807-2014

Radu, D.D., Duval, T.P., 2018. Precipitation frequency alters peatland ecosystem structure and CO2 exchange: Contrasting effects on moss, sedge, and shrub communities. Global Change Biology 24, 2051–2065. https://doi.org/10.1111/gcb.14057

Renssen, H., Seppä, H., Heiri, O., Roche, D.M., Goosse, H., Fichefet, T., 2009. The spatial and temporal complexity of the Holocene thermal maximum. Nature Geosci 2, 411–414. https://doi.org/10.1038/ngeo513

Riutta, T., Korrensalo, A., Laine, A.M., Link to external site, this link will open in a new window, Laine, J., Tuittila, E.-S., Link to external site, this link will open in a new window, 2020. Interacting effects of vegetation components and water level on methane dynamics in a boreal fen. Biogeosciences; Katlenburg-Lindau 17, 727–740. http://dx.doi.org.libproxy.helsinki.fi/10.5194/bg-17-727-2020

Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M., Tuittila, E.-S., 2007. Spatial variation in plant community functions regulates carbon

gas dynamics in a boreal fen ecosystem. Tellus B: Chemical and Physical Meteorology 59, 838–852. https://doi.org/10.1111/j.1600-0889.2007.00302.x

Ronkainen, T., McClymont, E.L., Tuittila, E.-S., Väliranta, M., 2014. Plant macrofossil and biomarker evidence of fen–bog transition and associated changes in vegetation in two Finnish peatlands. The Holocene 24, 828–841. https://doi.org/10.1177/0959683614530442

Ruppel, M., Väliranta, M., Virtanen, T., Korhola, A., 2013. Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe. The Holocene 23, 1596–1606. https://doi.org/10.1177/0959683613499053

Rydin, H., Jeglum, J.K., 2006. Biology of Peatlands. Oxford University Press, Oxford, UNITED KINGDOM.

Rydin, H., Mcdonald, A.J.S., 1985. Tolerance of Sphagnum to water level. Journal of Bryology 13, 571–578. https://doi.org/10.1179/jbr.1985.13.4.571

Saarnio, S., Morero, M., Shurpali, N.J., Tuittila, E.-S., Mäkilä, M., Alm, J., 2007. Annual CO2 and CH4 fluxes of pristine boreal mires as a background for the lifecycle analyses of peat energy. Boreal environment research 12, 101–113.

Sanderson, N., 2013. Lead-210 dating peat cores (University of Exeter No. University of Exeter), University of Exeter. University of Exeter, University of Exeter.

Schenk, F., Väliranta, M., Muschitiello, F., Tarasov, L., Heikkilä, M., Björck, S., Brandefelt, J., Johansson, A.V., Näslund, J.-O., Wohlfarth, B., 2018. Warm summers during the Younger Dryas cold reversal. Nat Commun 9, 1634. https://doi.org/10.1038/s41467-018-04071-5

Sillasoo, Ü., Väliranta, M., Tuittila, E.-S., 2011. Fire history and vegetation recovery in two raised bogs at the Baltic Sea. Journal of Vegetation Science 22, 1084–1093.

Silvola, Jouko, Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P.J., 1996. CO2 fluxes from peat in boreal mires under varying temperature and moisture conditions. The Journal of Ecology; Oxford 84, 219.

Silvola, J., Alm, J., Ahlholm, U., Nykanen, H., Martikainen, P.J., 1996. CO2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol. 84, 219–228. https://doi.org/10.2307/2261357

Song, L., Gilbert, D., Wu, D., 2016. Vertical micro-distribution of microbial communities living in Sphagnum fallax. Aquat. Microb. Ecol. 77, 1–10. https://doi.org/10.3354/ame01783

Strack, M., Waddington, J.M., Rochefort, L., Tuittila, E.-S., 2006. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. Journal of Geophysical Research: Biogeosciences 111. https://doi.org/10.1029/2005JG000145

Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J., Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T., Barr, I.D., Blaauw, M., Blundell, A., Chambers, F.M., Charman, D.J., Feurdean, A., Galloway, J.M., Gałka, M., Green, S.M., Kajukało, K., Karofeld, E., Korhola, A., Lamentowicz, Ł., Langdon, P., Marcisz, K., Mauquoy, D., Mazei, Y.A., McKeown, M.M., Mitchell, E.A.D., Novenko, E., Plunkett, G., Roe, H.M., Schoning, K., Sillasoo, Ü., Tsyganov, A.N., van der Linden, M., Väliranta, M., Warner, B., 2019. Widespread drying of European peatlands in recent centuries. Nat. Geosci. 12, 922–928. https://doi.org/10.1038/s41561-019-0462-z

Tahvanainen, T., 2011. Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment: Ombrotrophication of aapa mires. Journal of Ecology no-no. https://doi.org/10.1111/j.1365-2745.2010.01778.x

Taylor, R.E., 2000. Fifty Years of Radiocarbon Dating: This widely applied technique has made major strides since its introduction a half-century ago at the University of Chicago. American Scientist 88, 60–67.

Tolonen, K., Turunen, J., 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. Holocene 6, 171–178. https://doi.org/10.1177/095968369600600204

Tuittila, E.-S., Juutinen, S., Frolking, S., Väliranta, M., Laine, A.M., Miettinen, A., Seväkivi, M.-L., Quillet, A., Merilä, P., 2013. Wetland chronosequence as a model of

peatland development: Vegetation succession, peat and carbon accumulation. The Holocene 23, 25–35. https://doi.org/10.1177/0959683612450197

Tuittila, E.-S., Väliranta, M., Laine, J., Korhola, A., 2007. Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. Journal of Vegetation Science 18, 891–902. https://doi.org/10.1111/j.1654-1103.2007.tb02605.x

Turetsky, M.R., Donahue, W.F., Benscoter, B.W., 2011. Experimental drying intensifies burning and carbon losses in a northern peatland. Nat Commun 2, 1–5. https://doi.org/10.1038/ncomms1523

Turetsky, M.R., Kotowska, A., Bubier, J., Dise, N.B., Crill, P., Hornibrook, E.R.C., Minkkinen, K., Moore, T.R., Myers-Smith, I.H., Nykänen, H., Olefeldt, D., Rinne, J., Saarnio, S., Shurpali, N., Tuittila, E.-S., Waddington, J.M., White, J.R., Wickland, K.P., Wilmking, M., 2014. A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. Global Change Biology 20, 2183–2197. https://doi.org/10.1111/gcb.12580

Väliranta, M., Blundell, A., Charman, D.J., Karofeld, E., Korhola, A., Sillasoo, Ü., Tuittila, E.-S., 2012. Reconstructing peatland water tables using transfer functions for plant macrofossils and testate amoebae: A methodological comparison. Quaternary International, Peat Stratigraphy and Climate Change 268, 34–43. https://doi.org/10.1016/j.quaint.2011.05.024

Väliranta, M., Korhola, A., Seppä, H., Tuittila, E.-S., Sarmaja-Korjonen, K., Laine, J., Alm, J., 2007. High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: a quantitative approach. The Holocene 17, 1093–1107. https://doi.org/10.1177/0959683607082550

Väliranta, M., Salojärvi, N., Vuorsalo, A., Juutinen, S., Korhola, A., Luoto, M., Tuittila, E.-S., 2017. Holocene fen–bog transitions, current status in Finland and future perspectives. The Holocene 27, 752–764. https://doi.org/10.1177/0959683616670471

Väliranta, M., Salonen, J.S., Heikkilä, M., Amon, L., Helmens, K., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S., Veski, S., Birks, H.H., 2015. Plant macrofossil

evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. Nat Commun 6, 6809. https://doi.org/10.1038/ncomms7809

Vasander, H., 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Annales Botanici Fennici 19, 103–125.

Vitt, D.H., Halsey, L.A., Campbell, C., Bayley, S.E., Thormann, M.N., 2001. Spatial patterning of net primary production in wetlands of continental western Canada. Écoscience 8, 499–505. https://doi.org/10.1080/11956860.2001.11682680

Waddington, J.M., Roulet, N.T., 2000. Carbon balance of a boreal patterned peatland. Global Change Biology 6, 87–97. https://doi.org/10.1046/j.1365-2486.2000.00283.x

Waddington, J.M., Roulet, N.T., 1996. Atmosphere-wetland carbon exchanges: Scale dependency of CO2 and CH4 exchange on the developmental topography of a peatland. Glob. Biogeochem. Cycle 10, 233–245. https://doi.org/10.1029/95GB03871

Walker, T.N., Ward, S.E., Ostle, N.J., Bardgett, R.D., 2015. Contrasting growth responses of dominant peatland plants to warming and vegetation composition. Oecologia 178, 141–151. https://doi.org/10.1007/s00442-015-3254-1

Westra, S., Fowler, H.J., Evans, J.P., Alexander, L.V., Berg, P., Johnson, F., Kendon, E.J., Lenderink, G., Roberts, N.M., 2014. Future changes to the intensity and frequency of short-duration extreme rainfall. Reviews of Geophysics 52, 522–555. https://doi.org/10.1002/2014RG000464

Yu, Z., 2011. Holocene carbon flux histories of the world's peatlands: Global carbon-cycle implications. The Holocene 21, 761–774. https://doi.org/10.1177/0959683610386982

Yu, Z., Beilman, D.W., Jones, M.C., 2009. Sensitivity of northern peatland carbon dynamics to holocene climate change. Geophysical Monograph Series 184, 55–69. https://doi.org/10.1029/2008GM000822

Yu, Z., Loisel, J., Turetsky, M.R., Cai, S., Zhao, Y., Frolking, S., MacDonald, G.M., Bubier, J.L., 2013. Evidence for elevated emissions from high-latitude wetlands contributing to high atmospheric CH4 concentration in the early Holocene. Global Biogeochemical Cycles 27, 131–140. https://doi.org/10.1002/gbc.20025

Yu, Z.C., 2012. Northern peatland carbon stocks and dynamics: a review. Biogeosciences; Katlenburg-Lindau 9, 4071. http://dx.doi.org.libproxy.helsinki.fi/10.5194/bg-9-4071-2012

Zhang, H., Väliranta, M., Piilo, S., Amesbury, M.J., Aquino-López, M.A., Roland, T.P., Salminen-Paatero, S., Paatero, J., Lohila, A., Tuittila, E.-S., 2020. Decreased carbon accumulation feedback driven by climate-induced drying of two southern boreal bogs over recent centuries. Global Change Biology 26, 2435–2448. https://doi.org/10.1111/gcb.15005